Biological Reference Points for Anadromous Alewife (*Alosa pseudoharengus*) Fisheries in the Maritime Provinces

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TABLE OF CONTENTS

ABSTRACT/RESUMÉ v
INTRODUCTION 1
ASSESSMENT MODELS 3
METHODS 3
The Margaree River 3
The Miramichi River 4
The Mactaquac Headpond 4
The Gaspereau River 4
RESULTS 5
Mactaquac Headpond 5
The Margaree River 5
The Gaspereau River 6
The Miramichi River 6
Instantaneous Natural Mortality 6
Maturity Schedules 6
POPULATION DYNAMICS, PRODUCTION AND REFERENCE POINTS 7
METHODS 7
The Spawner-Recruit Model 7
The Spawning Biomass per Recruit Model 8
Reference Points 9
Decision Theoretic Approaches 10
RESULTS 12
SIMULATION MODELS 15
METHODS 15
Effects of Variable Maturity on Reference Points for Alewife 15
Evaluation of Reference Points with the Simulation Model 16
RESULTS 16
DISCUSSION 17
ACKNOWLEDGMENTS 20
REFERENCES 21
TABLES 26
FIGURES 29

ABSTRACT

Anadromous alewife, *Alosa pseudoharengus,* support commercial fisheries in many rivers in eastern North America. We analyzed the population dynamics of four alewife populations in the Maritime Provinces to evaluate reference points for the management of these fisheries. Spawner-recruit parameters and the resulting production model reference points are poorly determined for these populations when estimated from individual datasets. F_{msy} exceeds the fishing mortality rate that maximizes the expectation of the catch across a reasonable range of spawner-recruit parameter values and is not a good reference point for management of these populations.

Results of Monte Carlo population simulations show that fishing rates targeted not to exceed $F_{35\%}$ are probably reasonable strategies for alewife in the Maritime Provinces. This rate was less than F_{msy}, but still produced greater than 90% of the maximum median catch for all populations. It is therefore precautionary if the maximum annual reproductive rates were over-estimated in this study, but is not overly conservative because it produces a catch close to maximum sustainable yield if the estimates of the maximum annual reproductive rates are close to their true values. The average exploitation rate corresponding to $F_{35\%}$ is 0.39 for these populations. This is lower than the current limit reference point used in the Scotia-Fundy region (0.65), but similar to the reference point used in the Gulf Region.

RESUMÉ

Le gaspareau anadrome (*Alosa pseudoharengus*) fait l'objet d'une pêche commerciale dans de nombreuses rivières de l'est de l'Amérique du Nord. Nous avons analysé la dynamique de quatre populations de gaspareaux des provinces maritimes afin d'évaluer les points de référence pour la gestion de la pêche commerciale de cette espèce. Pour ces populations, les jeux de données individuels ne permettent pas de bien estimer les paramètres de la relation reproducteurs-recrues ni les points de références du modèle de production qui en résultent. Puisque le taux F_{REM} dépasse le taux de mortalité par pêche qui maximise les prises prévues pour un intervalle raisonnable de valeurs des paramètres de la relation reproducteurs-recrues, il ne constitue pas un bon point de référence pour la gestion de ces populations.

Les résultats des simulations de populations de type Monte Carlo montrent que des taux de prises qui ne dépassent pas $F_{35\,\%}$ constituent probablement des stratégies raisonnables pour le gaspareau des provinces maritimes. Ce taux était inférieur à F_{REM}, mais il a quand même donné un nombre médian de prises supérieur à 90 % du maximum pour chacune des populations. Ce taux est donc prudent si nos estimations des taux de reproduction annuels maximums sont trop élevées. Il ne l'est toutefois pas trop si nos estimations sont semblables à la réalité puisqu'il donne un nombre de prises s'approchant du rendement équilibré maximal. Le taux d'exploitation moyen qui correspond à $F_{35\,\%}$ est de 0,39 pour ces populations. Ce taux est inférieur au point de référence limite actuel utilisé dans la région de Scotia-Fundy (0,65), mais semblable au point de référence utilisé dans la région du Golfe.

INTRODUCTION

Alewife, *Alosa pseudoharengus,* is an anadromous species of fish that is indigenous to many rivers in eastern North America. Adults of this species ascend rivers during the spring and spawn in lakes, pools or stillwaters within the watershed. Young-of-the-year remain in fresh water until mid-summer to late fall when they migrate to the sea. Fish mature at 2 to 6 years of age, and maturity schedules vary among populations and years. The species is iteroparous and may spawn up to 5 times over a lifespan of about 10 years (Loesch 1987).

Alewife support both directed and by-catch commercial fisheries during coastal migrations along the eastern seaboard, and are fished both recreationally and commercially as they ascend natal rivers to spawn during the spring (Rulifson 1994). Ecologically, they are a prey species at sea and in fresh water, and are an important predator that can alter zooplankton community composition within lakes (Mills et al. 1992). They can also serve as a vector for nutrient transport from the oceans to inland waters (Durbin et al. 1979, Garman 1992, Garman and Macko 1998). As a result, over-exploitation or extirpation of alewife populations may alter the productivity of their natal watersheds, including production of freshwater and other anadromous fish.

Reported landings in the Maritime Provinces peaked in 1980 at just less than 11,600 t, and averaged 6,231 t between 1997 and 1999 (DFO 2001). Several stocks in this region exhibit characteristics of over-exploited stocks (Robichaud-LeBlanc and Amiro 2001). The Canadian Endangered Species Conservation Council lists the species as sensitive ("may require special attention or protection to prevent them from becoming at risk") within Nova Scotia (CESCC 2000) due to the uncertain effects of acid rain on this species.

Management strategies currently differ within the Maritime Provinces. In the absence of stock specific biological and fisheries information, the management objective is to maintain harvests at about their long-term mean levels (DFO 2001). Where information is available, populations in the Gulf Fisheries Management Region are managed on the basis that fishing mortality rates should not exceed the natural mortality rates, based on a review of several reference points (Chaput and Atkinson 1997). For the Margaree River, the instantaneous fishing mortality rate (F) is targeted not to exceed 0.4 (Chaput, LeBlanc and Crawford 2001), whereas on the Miramichi River, the fishing mortality for alewife is targeted in the range of 0.4 to 0.5 (Chaput and Atkinson 2001). In the Scotia-Fundy Fisheries Management Region, exploitation rates (u) are targeted not to exceed the average u_{msy} (0.65, corresponding to $F = 1.0$) calculated by Crecco and Gibson (1990) for 9 alewife stocks. Whether the biology of the Gulf and Scotia-Fundy stocks is sufficiently different to warrant these different management strategies is unknown.

Biological reference points (BRPs) are indices, based on the biological characteristics of a fish stock, that are used to gauge whether specific management objectives, such as maintaining stocks at a level capable of producing long term

maximum sustainable yield (MSY), are being achieved. Here, our purpose is to evaluate reference points for alewife fisheries in the Gulf and Scotia-Fundy regions through an analysis of the population dynamics of four alewife populations in the Maritime Provinces. Two of these populations spawn in watersheds that flow into the Gulf of St. Lawrence (the Margaree River and Miramichi River populations), and two spawn in watersheds that flow into the Bay of Fundy (the Mactaquac Headpond and Gaspereau River populations).

In the first section, we use a statistical, life-history based assessment model (Gibson and Myers in press[1]) to produce spawner-recruit (SR) time series and estimate maturity schedules, exploitation rates and natural mortality for these populations. We use the output from these models to analyse the dynamics of these populations in the following sections. The alternative, to estimate the production parameters within the assessment model has the advantage that uncertainty in the assessment model, is carried through the analysis, but has the disadvantage that additional model structure is added to the population reconstruction.

In the second section, we estimate reference points for the alewife populations using yield per recruit, spawning biomass per recruit and production models. We begin by using maximum likelihood methods to produce point estimates for several commonly used reference points. Focusing on the production model, we use profile likelihoods to assess the plausibility of values for the resulting reference points. We find that there is considerable uncertainty in the resulting reference point estimates and that the maximum likelihood point estimates (MLEs) are not a reasonable basis for management as a result. Ianelli and Heifetz (1995) describe a decision theoretic method of estimating a reference point that maximizes the expectation of the catch by integrating across the likelihood surface for the SR parameters. This approach explicitly incorporates uncertainty in the model parameters in the estimation of the reference points. We use a similar approach to estimate the fishing mortality rate that maximizes the expectation of the catch for these alewife populations, and extend the approach to include data from other alewife populations in the estimation of a probability surface for the SR parameters.

Process variability (variability around the SR relationship and variability in maturity schedules) can substantially alter the size of in-river spawning migrations from year to year. We evaluate how process variability affects the performance of reference points in the third section. Here, we use a simulation model to evaluate the relationship between target fishing mortality rates and the performance of the fisheries when stochastic variability is added to the recruitment process. Additionally, we compare simulations with stochastic variability in the maturity schedule with simulations using constant maturity schedules to determine whether failure to consider variability in age at maturity can lead to over-exploitation of these stocks.

ASSESSMENT MODELS

METHODS

Fournier and Archibald (1982) and Deriso et al. (1985) developed the general theory for statistical catch-at-age models for stock assessment that allow auxiliary data to be incorporated into the model. Following their approach, we used a statistical, life history based stock assessment model for anadromous *Alosa* (Gibson and Myers, in press[1]) to model the number of fish in the spawning run in each year by sex (Gaspereau River and Mactaquac Headpond populations only), age and previous spawning history, and to estimate annual exploitation rates, the instantaneous natural mortality rate, and maturity schedules for each of the four populations. While the basic model structure is similar for each population, the types of data available differ among populations, and population-specific adaptations are necessary as a result. Details of the models, described below, are shown in Table 1. The data available for each population are provided in Table 2.

We ran these models using AD Model Builder (Fournier 1996). AD Model builder uses the C++ auto-differentiation library for rapid fitting of complex non-linear models, has Bayesian and profile likelihood capabilities, and is designed specifically for fitting these types of models.

The Margaree River

Of primary interest is the number of fish returning to the river in year t, of sex s, age a, that have spawned p times previously, which we denote $N_{t,s,a,p}$. The data for the Margaree River alewife fishery consists of the total catch (C_t) for the years 1983 to 2000, an estimate of the number of fish in each age and previous spawning history category ($C_{t,a,p}$), reported for both sexes combined (we therefore drop the subscript s from the notation for this population). A larval index is also available that may be interpreted as an index of spawner abundance, and has been used in the catch-at-age analyses in assessments of this stock (Chaput et al. 2001) We initially included the larval index in the model, but found that its inclusion produced estimates of natural mortality that were negative (abundance with a cohort increasing through time). It also induced a retrospective pattern in the predicted exploitation rates, and produced estimates of exploitation rates that were lower than those estimated without the larval index. Merritt and Quinn (2000) suggest that conservatism and the biological plausibility of parameter estimates are two criteria that can be used to select between alternative models and to assess auxiliary data. The larval index produced estimates of the exploitation rates that were less conservative and implausible estimates of natural mortality, so we removed the larval index from the model.

Alewife in the Margaree River mature between 2 and 6 years of age, with the majority maturing at ages 3 and 4. We set up the model (Table 1) to estimate the number of first time spawners in each age class (ages 2 to 6) in each year ($N_{t,a,0}$), the exploitation rate in each year (u_t), assumed constant across ages, and the instantaneous rate of natural mortality for mature fish (M^{adult}). We assumed M^{adult} constant across age and year classes.

The relationship between the instantaneous rate of fishing mortality, F_t, and u_t is $F_t = -\log(1-u_t)$. Spawning escapement by year, age and previous spawning category, $E_{t,a,p}$, is given by $N_{t,a,p}$ multiplied by the compliment of the exploitation rate in year t. The spawner biomass in year t, SSB_t, is the sum of $E_{t,a,p}$ multiplied by the weight at age, w_a. We fit the model to the data by minimizing an objective function (*O.B.V.*) that is the sum of the non-constant portions of the negative log likelihoods for the catch (ℓ_{catch}) and number of fish in each year-age-previous spawning category ($\ell_{composition}$). The relative contribution of each likelihood to the objective function was controlled using a set of weighting values, λ_i, selected to keep any one part of the objective function from dominating the fit. We used a lognormal error structure for the catch (C_t^{obs} and C_t are the observed and predicted catches in year t) and a multinomial error structure for the number of fish in each year, age and previous spawning category ($n_{t,a,p}^{obs}$ is the observed number of fish of age a that have spawned p times previously within a sample collected in year t, and $p_{t,a,p}$ is the predicted proportion of fish in each age and previous spawning catagory in that year).

The Miramichi River

The model used for the Miramichi River population is identical to that for Margaree River alewife with the exception that the ages at maturity for the later population were age 3 to 6.

The Mactaquac Headpond

The data for the Mactaquac Headpond population consists of estimates of the catch and spawning escapement in each year, and estimates of the spawning run composition by sex, age and previous spawning history. The model is similar to that described above, with the exceptions that we used a two-sex model, and a third log likelihood was added to the objective function to fit to the observed spawning escapements (E_t^{obs} and E_t are the observed and predicted spawning escapements respectively). We used a lognormal error structure for the escapement data.

The Gaspereau River

Biological data for the Gaspereau River population is limited. There is a 10 year period when only the catch was reported (Table 2). We wanted estimates of the population size and age composition during this time period, which we obtained using two restrictive assumptions. First, we treated the exploitation rate as known, rather than estimating the exploitation rates in each year (as above). For years when the escapement counts are available, we calculated the annual exploitation rate directly by dividing the catch by the sum of the catch and the escapement count. For years when no data other than the catch is available, we used the mean of the calculated exploitation rates (the fishery has been conducted in a similar manner throughout this time period). Second, rather than estimating $N_{t,s,a,0}$ (as above), we estimated the number of age-3 recruits (R_{t-a+3}) in each year and a maturity schedule for each sex ($m_{s,a}$, for a ranging from 3 to 6).

The maturity schedules were assumed constant among years, an assumption that is not made for the other populations. We assumed that the sex ratio, υ_s, is 1:1 at age three. These approaches reduce the number of parameters to be estimated relative to the other populations and allow abundance at age and previous spawning history to be estimated.

RESULTS

Mactaquac Headpond

Summaries of the assessment model output for the four populations are shown in Figures 1 to 8. The population is divided into "sub-cohorts" (designated by cohort year, age-at-maturity and sex in the two sex model) and the abundance of each sub-cohort is followed through time. For the Mactaquac Headpond population, the observed data shows increasing abundance through time for some sub-cohorts, particularly between the first and second spawnings (Figure 1). We believe this pattern may result from not all first time spawning fish ascending the river to the base of the dam. This pattern is less evident in more recent years (we only show part of the escapement-at-age array in Figure 1). During the mid 1970's and early 1980's the estimated spawning escapement is higher than the observed escapement count as a result (Figure 2), and the observed harvest fraction (calculated as the catch divided by the sum of the catch and the escapement count) is higher than the estimated exploitation rates during this period. This pattern is not evident in late 1980's and 1990's, suggesting some non-stationarity in the process generating these data. Our resulting SR time series (predicted spawner abundance and recruitment) differs from that used by other authors for the same data. For example, Jessop (1990) used the observed escapement count as a measure of spawner abundance and calculated the number of age-3 recruits from the observed number of first time spawners in each sub-cohort. Exploitation rates for this population have varied between 19% and 63% during the 1990's.

The increase in the observed abundance within a sub-cohort through time was not evident in data for the Margaree River (Figure 3), the Gaspereau River (Figure 5) or the Miramichi River (Figure 7). These fisheries are executed much closer to the river mouths than the fishery for the Mactaquac Headpond population.

The Margaree River

For the Margaree River, the predicted catch-at-age and predicted total catch fit the observed catch-at-age (Figure 3) and total catch (Figure 4) very closely. During this time period, the catch on this river peaked at 1,912 t in 1988, after which the population size declined (Figure 4). High exploitation rates during the early 1990's led to increased within season closed periods implemented in 1996. These closures have reduced exploitation rates from an average of 0.81 (1991 to 1995 time period) to 0.56 (1996 to 2000). These rates are higher than those estimated when the larval index is used to tune the model (e.g. Chaput et al. 2001). Spawning escapement has increased slightly as a result of the increased within season closures, but is still lower than the levels predicted for the 1980's (Figure 4).

The Gaspereau River

Other than the catch and an escapement count in 1995, the Gaspereau River alewife data is limited to the years 1982 to 1984 and 1997 to 2001, and some restrictive assumptions were necessary in order to estimate numbers in each sub-cohort (Gibson and Myers 2001). The resulting fit to the observed escapement-at-age for the Gaspereau River (Figure 5) is not as good as for the Margaree River. The predicted catch and spawning escapements show the second highest abundance in 1987, one of the lowest abundances in 1988 and the highest abundance in 1989 (Figure 6). This pattern probably indicates that the constant exploitation rate or constant maturity schedule assumptions are not appropriate during one or more of these years. For this reason we did not include data for these years in the resulting SR time series. Exploitation rates for this population averaged 83 % between 1997 and 2000. The lower exploitation rate in 2001 (38 %) was the result of high water levels in the river during that year.

The Miramichi River

For the Miramichi River, the predicted catch-at-age and total catch fit the observed catch-at-age (Figure 7) and the observed catch (Figure 8) quite closely. Predicted spawning escapements peaked in 1986 and have been at low levels since 1995 (Figure 8). Predicted exploitation rates for this population averaged 68 % from 1990 to 2000, and 76 % from 1996 to 2000 (Figure 8).

Instantaneous Natural Mortality

Estimates of the instantaneous rate of natural mortality for adult fish ranged between 0.25 for the Mactaquac Headpond to 0.53 for the Gaspereau River (Table 3). We believe that the low estimate for the Mactaquac Headpond is inaccurate due to the issue of increasing abundance within a sub-cohort that is not completely addressed within the assessment model. We used the value of M^{adult} for the Gaspereau River for the Mactaquac Headpond population in the reference point calculations and simulation modelling for this reason. The estimates for the Gaspereau River and Mactaquac Headpond are further confounded because these rivers are modified for hydroelectric generation and estimates of turbine mortality are not available for these rivers. The standard errors (based on the assumption of asymptotic normality) for the Gaspereau River, Margaree River and Mactaquac Headpond suggest that these parameters are well estimated for these rivers. However, the profile likelihood for M^{adult} for the Margaree River (not shown) indicates that the asymptotic approximation is not very good for this river and that the lower bound for M^{adult} is not well determined. This is probably due to the confounding effects of simultaneously estimating u_t and M^{adult} without auxiliary data. However, the estimates of M^{adult} for the Margaree and Miramichi River are similar to that obtained by Chaput and Alexander (1989) of 0.44 between the first and second spawnings for alewife in the South River. The asymptotic approximations closely matched the profile likelihoods for M^{adult} for the Gaspereau River and Mactaquac Headpond (auxiliary data is available in the form of escapement counts for these populations).

Maturity Schedules

Maturity schedules differ between alewife populations in the Gulf of St. Lawrence and the Bay of Fundy. Most alewife in the Gulf region mature at ages 3 or 4 (Table 3),

and the majority of variability in age at maturity occurs at age 3 (Figure 9). Most alewife in the Bay of Fundy populations mature at ages 4 and 5 (Table 3), and most of the variability for the Mactaquac population occurs at age 4 (Figure 9). The Gaspereau River data is not sufficient to estimate a separate maturity schedule for each cohort.

POPULATION DYNAMICS, PRODUCTION AND REFERENCE POINTS

METHODS

We modelled the population dynamics of alewives using two equations, a spawner-recruit relationship that expresses recruitment as a density dependent function of spawner biomass, and the replacement line, the slope of which is the inverse of the rate at which recruits produce replacement spawners. Here, an implicit assumption is made that all density-dependent processes occur between spawning and recruitment. This assumption is consistent with the concentration hypothesis (Beverton 1995) and population regulation in American shad (Savoy and Crecco 1988). We therefore choose the age of recruitment to be 3 (the earliest age of maturity for most stocks and the latest age that could be chosen prior to fish entering the fisheries), and defined recruitment for year class t, R_t, as:

$$R_t = \sum_{a=3}^{6} \left(N_{t+a,a} / e^{-M^{juv}(a-3)} \right).$$

Here, $N_{t+a,a}$ is the number of fish of age a, in year $t+a$, that are returning to the river to spawn for the first time, and M^{juv} is the instantaneous natural mortality rate of immature alewife while at sea. We do not have the data to estimate M^{juv} within the models and assumed a constant value of 0.4 based on the empirical relationship between longevity (maximum age of 11 years) and natural mortality developed by Hoenig (1983).

The Spawner-Recruit Model

We modeled the rate at which spawners produce recruits using the Beverton-Holt spawner-recruit model. This model and Ricker model are the most commonly used two parameter spawner-recruit models (Hilborn and Walters 1992). These models differ fundamentally in their assumptions of the underlying biology, the later showing a decline in recruitment at higher spawner abundance, a phenomenon known as overcompensation. In a meta-analysis of the population dynamics of anadromous *Alosa*, Gibson and Myers (in press[2]) found that the Beverton-Holt model provided a consistently better fit to alewife spawner-recruit data than did the Ricker model. The Beverton-Holt spawner-recruit model gives R_t as a function of the spawning biomass in year t, SSB_t:

$$R_t = \frac{\alpha SSB_t}{1 + (\alpha SSB_t / R_0)}.$$

Here, α is the slope at the origin, and in the deterministic model is the maximum rate at which spawners can produce recruits at low population sizes (Myers et al. 1999) and R_0 is the asymptotic recruitment level (expressed as the number of age-3 recruits). R_0 is the limit approached by R_t as S_t approaches infinity (Beverton-Holt models are often written in terms of the half saturation constant, K, which is related to R_0 by: $R_0 = \alpha K$). Parameter

estimates for each population were obtained by using maximum likelihood assuming a lognormal error structure for recruitment (Myers et al. 1995). Denoting the Beverton-Holt spawner-recruit function as $g(s_i)$, the log-likelihood is given by:

$$\ell(\alpha, R_0, \sigma) = -n \log \sigma\sqrt{2\pi} - \sum \log r_i - \frac{1}{2\sigma^2} \sum \log\left(\frac{r_i}{g(s_i)}\right)^2$$

where s_i and r_i are the observed spawner biomass and recruitment data, σ is the shape parameter and n is the number of paired SR observations. We use profile likelihoods to assess the plausibility of the individual parameter estimates given the data. The log profile likelihood for α, $\ell_p(\alpha)$, is:

$$\ell_p(\alpha) = \max_{R_0 \sigma} \ell(\alpha, R_0, \sigma).$$

The MLE for α occurs where $\ell_p(\alpha)$ achieves its maximum value. The plausibility of other possible values of α was evaluated by comparing their log likelihoods with the maximized log likelihood. A likelihood based 95% confidence interval for α was calculated as:

$$\{\alpha : 2\left[\ell_p(\alpha^{\text{MLE}}) - \ell_p(\alpha)\right] \le \chi_1^2(0.95)\}.$$

The profile likelihood and the associated 95% confidence interval for R_0 were found similarly.

The Spawning Biomass per Recruit Model

We modelled the rate at which recruits produce spawners (the inverse of the slope of the replacement line) by calculating the spawning biomass per recruit (*SPR*) as a function of fishing mortality (Shepherd 1982, Mace and Sissenwine 1993, Mace 1994). The model is an extension of a yield per recruit model (Beverton and Holt 1957), that we have adapted for alewife life history:

$$SPR_F = \sum_{a_{rec}}^{a_{max}} SS_a w_a e^{-F}$$

where SS_a is given by:

$$SS_3 = m_3$$

$$SS_4 = SS_3 e^{-(M^{adult} + f)} + (1 - m_3) e^{-M^{juv}} m_4$$

$$SS_5 = SS_4 e^{-(M^{adult} + f)} + (1 - m_3)(1 - m_4) e^{-2M^{juv}} m_5$$

$$SS_6 = SS_5 e^{-(M^{adult} + f)} + (1 - m_3)(1 - m_4)(1 - m_5) e^{-3M^{juv}} m_6$$

.

.

$$SS_{a_{max}} = SS_{a_{max}-1} e^{-(M^{adult} + f)} + (1 - m_3)(1 - m_4)\ldots(1 - m_{a_{max}-1}) e^{-(a_{max}-3)M^{juv}} m_{a_{max}}$$

Here, a is the age of the fish and m_a is the probability that a fish that is alive at age a will mature at that age.

The Production Model

For a given value of F, the spawning biomass produced by the number of recruits in year t is $SSB = SPR_F \cdot R_t$. Equilibrium spawning biomasses and recruitment levels (denoted with asterisks) were found by solving this equation for R_t, and substituting the result in the spawner-recruit model (Quinn and Deriso 1999):

$$\frac{SSB^*}{SPR_F} = \frac{\alpha SSB^*}{1+\frac{\alpha SSB^*}{R_0}}.$$

The equilibrium spawning biomass (SSB^*) is then:

$$SSB^* = \frac{(\alpha SPR_F - 1)R_0}{\alpha},$$

and the equilibrium number of recruits (R^*) is found by substituting the SSB^* in the spawner-recruit model:

$$R^* = \frac{\alpha SSB^*}{1+\frac{\alpha SSB^*}{R_0}}.$$

The equilibrium catch (C^*) is R^* multiplied by the yield per recruit for the given value of F:

$$C^* = R^* \cdot YPR_F.$$

Here, the yield per recruit for a given F (YPR_F) is found analogously to the spawning biomass per recruit for a given F described above:

$$YPR_F = \sum_{a_{rec}}^{a_{max}} SS_a w_a (1 - e^{-F}) \ .$$

Reference Points

Reference points from the spawning biomass per recruit and yield per recruit analyses were found using a grid search across a set of F's {0,0.05,0.1,0.15,.....4.0}. We calculated YPR_F and SPR_F for each value of F, and reference points were then estimated by selected the fishing mortality rate corresponding to the appropriate reference point criterion. The yield per recruit reference point, F_{max} was found by selecting the fishing mortality rate where YPR_F takes its largest value, and $F_{1.0}$ was found by selecting the fishing mortality rate where the marginal gain in yield was 10% that at F=0. The $SPR_{x\%}$ reference points were found by selecting the fishing mortality rate where the SPR_F was x% that of $SPR_{F=0}$.

Sissenwine and Shepherd (1987) suggested that where SR relationships are poorly determined, an alternative reference point based on SR data, F_{rep}, can be found by finding the fishing mortality rate that produces a replacement line with a slope that equals the average survival ratio. They suggested it could be estimated from the median survival ratio in which case it is often referred to as F_{med} (Quinn and Deriso 1999). It is then the level of fishing mortality where recruitment has been more than sufficient to balance losses to fishing mortality in half the observed years (Jacobsen 1993). The related reference points, F_{low} and F_{high}, are the fishing mortality rates where recruitment has been sufficient to offset fishing mortality in one year out of ten and nine years out of ten

respectively. We found F_{med}, F_{high} and F_{low} by calculating the slope of the replacement line through each point in the SR time series, selecting the 10th, 50th and 90th percentiles of these slopes and selecting the fishing mortality rates that produce replacement lines with these slopes from the SPR_F vector.

We estimated five reference points from the production model. The equilibrium spawning biomass in the absence of fishing, SSB_{eq}, was estimated directly from the production model. A spawning biomass of 20% SSB_{eq} is often used as a minimum threshold population size (Beddington and Cooke 1983, Goodyear 1993). $SSB_{20\%}$ was calculated as 20% the equilibrium spawner abundance in the absence of fishing:

$$SSB_{20\%} = 0.2\frac{(\alpha SPR_{F=0} - 1)R_0}{\alpha}$$

Grid searches were used to find the fishing mortality rate that produces maximum sustainable yield (F_{msy}), the corresponding spawner biomass that produces maximum sustainable yield (SSB_{msy}) and the fishing mortality rate that drives the population to extinction (F_{col}). We estimated F_{msy} by calculating C^* for each value of F, and selecting the value where C^* was maximized. SSB_{msy} was the value of S^* corresponding to this fishing mortality rate. The equilibrium fishing mortality rate at which the population goes extinct, F_{col}, is determined by the slope of the SR relationship at the origin α, and is the value of F where $1/SPR_{F=0} = \alpha$.

Decision Theoretic Approaches

The profile likelihoods and likelihood surfaces for the SR models show that the SR parameters and hence the corresponding production model reference points are not well determined for these alewife populations (see Results). Clark (1991) suggested that a production-based reference fishing mortality rate (F_{mmy}) could be estimated without any knowledge of the true SR model by maximizing the minimum yield across a reasonable range of α's. In a meta-analysis of the population dynamics of alewife, Gibson and Myers (in press[2]) provided probability distributions for the natural logarithms of lifetime maximum reproductive rate and carrying capacity for alewife at the species level. We updated their analysis (see results) and used the 0.1st and 99.9th percentiles from these distributions to obtain upper and lower limits for the annual reproductive rate (α), and calculated the yield for each F for α at these limits. F_{mmy} was found by selecting the fishing mortality rate that maximized the minimum yield from the two resulting yield curves.

The profile likelihoods and likelihood surfaces for the SR models show that R_0 is not precisely estimated for these populations (see Results). Consequently, the data do not preclude the possibility that these populations could be substantially larger than at the maximum likelihood estimates. Larger population sizes would lead to larger yields from the fishery, and given the uncertainty in the parameter estimates, a reference point based on the maximum likelihood estimates for the parameters would be inappropriate if it reduced the probability of obtaining larger catches. As an alternative, a set of plausible SR parameters can be viewed as a set of alternative hypotheses about the productivity of each stock, and a reference point can be defined as the fishing mortality rate that

maximizes the expectation of the equilibrium catch over this set of alternative hypotheses (Ianelli and Heifetz 1995). We call this point $F_{max.E(C)}$.

We set up a parameter space, Ω, for the SR model with two dimensions: α and R_0. Each point in this parameter space represents a separate hypothesis about the productivity of the population. We used $\alpha = \frac{1}{SPR_{F=0}}$ as the lower limit for α for each population. Below this limit, reproduction would not be sufficient to offset natural mortality and the population would go extinct. We set the upper bound for α at 250. We used the 1st and 99th percentiles of the random effects distribution of R_0 for the bounds on R_0. Treating the maturity schedules and non-fishing mortality rates as constants, the expectation of the equilibrium catch is:

$$E(C^*(F)) = \int\int C^*(F,\alpha,R_0)p(\alpha,R_0)dR_0 d\alpha$$

where $C^*(F,\alpha,R_0)$ is the equilibrium catch as a function of the fishing mortality rate, the maximum reproductive rate and the asymptotic recruitment level, and $p(\alpha,R_0)$ is the probability density evaluated at α and R_0. Here, $E(C^*(F))$ is the expectation of the equilibrium catch for a given F evaluated by integrating over the uncertainty in the estimates of α and R_0. The fishing mortality rate that maximizes the expectation of the catch is then:

$$F_{\max E(C)} = \underset{F}{\text{argmax}}\ E(C^*(F)) .$$

We calculated $p(\alpha,R_0)$ four ways:

1. Treating all points in $\{\alpha,R_0\}$ as equally probable:

$$p(\alpha,R_0) = \begin{cases} c, & \alpha,R_0 \in \Omega \\ 0, & \text{otherwise} \end{cases}$$

where c is a positive constant. This approach to estimating $F_{max.E(C)}$ is similar to the method for estimating F_{mmy} (Clark 1991) in that no information other than the bounds on the SR parameters are used to estimate the reference point. It differs from F_{mmy} by including R_0 as well as α in the estimation procedure, and by maximizing the expectation of the catch rather than maximizing the minimum yield across a set of α's.

2. Using the random effects distributions for α and R_0 as priors:

$$p(\alpha,R_0) = \begin{cases} \dfrac{p(\alpha)\cdot p(R_0)}{\iint_{\Omega} p(\alpha)\cdot p(R_0)d\alpha dR_0}, & \alpha,R_0 \in \Omega \\ 0 & \text{otherwise} \end{cases}$$

Myers et al. (2002) demonstrate how informative prior distributions can be estimated for SR parameters from information about taxonomically similar populations, ecologically similar populations and from life history and environmental data. In the absence of stock specific information, these priors can be used as a basis for management. Here, we use the random effects distributions

for α and R_0 from a meta-analysis of eight alewife populations. This approach is preferable to the first method because the priors can be used to place bounds on the parameters and is more reasonable than assuming that all parameter values are equally probable.

3. Using the likelihood surface for each population:

$$p(\alpha, R_0) = \left\{ \begin{array}{ll} \dfrac{L(\mathbf{R} \mid \mathbf{S}, \alpha, R_0)}{\iint_{\Omega} L(\mathbf{R} \mid \mathbf{S}, \alpha, R_0) d\alpha dR_0}, & \alpha, R_0 \in \Omega \\ 0 & \text{otherwise} \end{array} \right\}$$

This approach uses only stock specific data. The resulting estimate of $F_{max.E(C)}$ differs from F_{msy} by finding the F that maximizes the expectation of the catch across the likelihood surface, rather than finding the MLE's of α and R_0 and calculating F_{msy}. This is similar to the approach of Ianelli and Heifetz (1995).

4. Combining the likelihoods and the priors to obtain the joint posterior distribution:

$$p(\alpha, R_0) = \left\{ \begin{array}{ll} \dfrac{L(\mathbf{R} \mid \mathbf{S}, \alpha, R_0) \cdot p(\alpha) \cdot p(R_0)}{\iint_{\Omega} L(\mathbf{R} \mid \mathbf{S}, \alpha, R_0) \cdot p(\alpha) \cdot p(R_0) d\alpha dR_0}, & \alpha, R_0 \in \Omega \\ 0 & \text{otherwise} \end{array} \right\}$$

This approach takes fullest advantage of both stock specific data and prior information about α and R_0.

RESULTS

Reference points for the 4 alewife populations are shown in Table 4. The fishing mortality rate that maximized the yield per recruit, F_{max}, was greater than 3.0 for all populations. $F_{0.1}$ was ranged between 0.71 for the Mactaquac Headpond population and 0.91 for the Margaree River population.

Because of differences in the maturity schedules, the spawning biomass per recruit in the absence of fishing for the Gulf populations was almost twice that of the Scotia-Fundy populations (Figure 10). However, the fishing mortality rates that reduced spawning biomass per recruit to 35% the level without fishing mortality was similar for all populations (range: 0.49 to 0.55). The reference points F_{med}, F_{high} and F_{low} varied between populations (Table 4), probably as a result of the different ranges of spawner abundances for each population (Figure 11). F_{low} equalled 0.0 for three of the four populations, indicating that recruitment was insufficient for replacement over the range of observed spawner abundances more than 10% of the time in these populations.

The fishing mortality rate that produces maximum sustainable yield, F_{msy}, estimated from the production model using the MLE's for α, ranged from 0.76 for the Mactaquac Headpond to >4.0 for the Miramichi River. The fishing mortality rate that drives the population to extinction, F_{col}, ranged from 1.53 for the Mactaquac Headpond to

>4.0 for the Miramichi River. The spawning biomass that produces maximum sustainable yield, SSB_{msy}, was less than $SSB_{20\%}$ for all populations except the Mactaquac Headpond (Table 4).

The relationships between the reference points from the production model are shown together with the SR data in Figure 11. The data for all populations show considerable variability about the fitted SR model. For the Gaspereau River, all spawner abundances are below $SSB_{20\%}$ and all but three observations are below SSB_{msy}. The pattern is similar on the Margaree River, where all but three spawner abundances are below SSB_{msy}.

The production model reference points were calculated using the MLE's from the SR model, and the resulting reference points are therefore only as good as the SR parameter estimates. Profile likelihoods (Figure 13) show that while the lower bound for a 95% confidence interval for alpha is determined for all populations, the upper bound is not determined for all populations except the Mactaquac Headpond (the profiles are ramped). Similarly, the 95% confidence interval for the asymptotic recruitment level is very wide for all populations. Profile likelihoods for the exploitation rate at MSY and SSB_{msy} are shown in Figure 13. Lower bounds on the 95% confidence interval for u_{msy} range from 0.24 (Margaree River and Mactaquac Headpond) to 0.32 for the Miramichi River. The upper bound for the 95% confidence interval (0.83) was only determined for the Mactaquac Headpond. Similarly, the lower bound on 95% confidence interval for SSB_{msy} could only be determined for the Mactaquac Headpond population.

Gibson and Myers (in press[2]) carried out a meta-analysis of the population dynamics of anadromous alewife to estimate probability distributions for SR parameters for alewife at the species level using a nonlinear mixed effects model. We have updated the SR time series used in their analysis to reflect the changes in the assessment modeling. Their analysis suggested that the Mactaquac Headpond population was very small (on a per unit area basis) relative to other alewife populations and that carrying capacity may not have been well determined for this population. Our re-analysis of the SR data showed that this population substantially increased the standard deviation of the random effects distribution for carrying capacity. We have reproduced their meta-analytic summary (our Figure 14) to show the changes in the SR time series and re-estimated the random effects distribution for the SR parameters without the Mactaquac Headpond population. Note that, in this analysis, alpha is lifetime maximum reproductive rate which is equivalent to the annual maximum reproductive rate multiplied by the $SPR_{F=0}$ in the deterministic case. The lifetime maximum reproductive rate is only well determined for two of the eight populations. For these populations, the maximum lifetime reproductive rate tends to be lower than for populations where the profile likelihood is ramped (the Mactaquac Headpond estimate may be confounded with turbine mortality of juvenile fish and/or fishing of adults in the lower river). Similarly, carrying capacity estimates with small confidence intervals tend to be higher than those that have larger confidence intervals. These patterns suggest that the maximum reproductive rates may be overestimated and carrying capacity underestimated for populations where the SR parameters are poorly determined. The random effects distribution for the log of the

lifetime maximum reproductive rate has a mean of 3.06 and a standard deviation of 0.1. The random effects distribution for the log of the carrying capacity has a mean of 4.01 and standard deviation of 0.41. These estimates suggest that at low population sizes and in the absence of anthropogenic mortality, one alewife can produce about 21.3 age-3 recruits throughout its life, and that the carrying capacity for a typical alewife population is about 55 t/km^2 of nursery area.

The likelihood surfaces for the SR parameters for all four Atlantic region populations contain a "L"-shaped ridge (Figure 15), along which the log-likelihood changes only slightly. In all populations, there are plausible values of alpha (not significantly difference from the MLE of alpha at a 95% confidence level) for which there is the possibility that the asymptotic recruitment level is substantially higher than the MLE for this parameter. This implies that the data do not preclude the possibility of larger recruitments, and that the subsequent catch could potentially increase if the fishing mortality rate was set below the MLE for F_{msy} (F_{msy} is poorly determined by the data for all populations). The data also suggest that larger population sizes are less plausible at the MLE for α (again poorly determined by the data) than at a lower maximum annual reproductive rate. As discussed, an appropriate reference fishing mortality rate should not preclude the possibility of achieving larger catches, particularly if the reference rate is not significantly different from the MLE of F_{msy}. Specifically, the fishing mortality rate that maximizes the expectation of the catch, $F_{max.E(C)}$, across a range of plausible SR parameter values, should be a better target fishing mortality rate than a rate based on a poorly determined MLE of F_{msy}, because it explicitly includes the uncertainty in the parameter estimates in the selection of the reference F.

This approach is illustrated in Figure 16. We converted the random effects distributions of the log lifetime maximum reproductive rate and log carrying capacity to probability distributions for the annual maximum reproductive rate and the asymptotic recruitment level. These distributions are plotted beside the SR parameter joint log likelihood surface for the Gaspereau River population. The prior distribution for α suggests that the very large population sizes that are not precluded by the likelihood surface are not very plausible. The priors for both α and R_0 suggest that a slightly lower maximum reproductive rate and higher asymptotic recruitment level are very plausible for this population.

The estimates of $F_{max.E(C)}$, shown in Table 5, vary depending on the method used to calculate $p(\alpha, R_0)$. $F_{max.E(C)}$ was less than F_{msy} for all populations except the Mactaquac Headpond (here, the low estimate of alpha and hence low estimate of F_{msy} is potentially a result of turbine mortality in the migratory juvenile life stage or fishing in the lower river). For all populations, the relationship between the exploitation rate and the expectation of the catch based on the joint posterior distribution was almost identical to the relationship calculated using only the priors from the meta-analysis (Figure 17). For populations with ramped profile likelihoods for α, the expectation of the catch calculated using only the likelihood surface implies that the fishery is sustainable at exploitation rates of greater than 99%. When calculated using the joint posterior distribution, none of the fisheries are sustainable at exploitation rates greater than 87% (Figure 17).

SIMULATION MODELS

METHODS

Effects of Variable Maturity on Reference Points for Alewife

The size of alewife spawning runs, and hence their availability to in river fishing is a function not only of recruitment and survival, but also of their maturity schedules, which can vary from year to year. A constant exploitation rate strategy, selected only on the basis of recruitment and survival, could substantially reduce spawner abundance in some years if maturity variability is a key determinant of run size. We investigated this possibility using a Monte Carlo simulation model based on the analysis for the Margaree River. Random variability was introduced into the model through the recruitment process, and simulations using constant and variable maturity schedules were compared to determine whether variability in age at maturity affected the resulting reference points. The model equations are:

$$R_{t+3} = \frac{\alpha SSB_t}{1+\frac{SSB_t}{K}} \exp\left(\varepsilon_t \sigma - \frac{\sigma^2}{2}\right), \quad where\ \varepsilon_t \sim N(0,1)$$

$$N_{t,a,0} = R_{t-a+3} m_a e^{-M^{juv}(a-3)} \quad \text{(see below for the calculation of } m_a\text{)}$$

$$E_{t,a,p} = N_{t,a,p}(1-u_t)$$

$$N_{t+1,a+1,p+1} = E_{t,a,p} e^{-M^{adult}}$$

$$C_{t,a,p} = N_{t,a,p} u_t$$

$$C_t = \sum_a \sum_p \left(N_{t,a,p} u_t\right)$$

$$SSB_t = \sum_a \sum_p (E_{t,a,p} w_a)$$

The parameters α, R_0, σ were obtained from the SR model, M^{adult} and the mean maturity schedules, m_a, from the assessment model. We did not find evidence of autocorrelation in the residuals of the SR models for any of the populations, and therefore treated the deviates around the SR relationship as uncorrelated. We mapped the probability that a fish that is alive at age a matures at age a to the real line using a logistic transformation:

$$\text{logit}(m_a) = \log\left(\frac{m_a}{1-m_a}\right).$$

For each cohort, logit(m_a) was calculated for age classes 2 to 5, and the mean and standard deviations of m_a for each age class were calculated to describe the maturity process. For simulations with variable maturity schedules, a random component was introduced on the logistic scale by drawing a random number from a normal distribution with the mean and standard deviation above. This value was back-transformed to obtain the random m_a:

$$m_a = \frac{\exp(\text{logit}(m_a) + \varepsilon_a)}{1 + \exp(\text{logit}(m_a) + \varepsilon_a)}, \text{ where } \varepsilon_a \sim N(0, \text{var}(\text{logit}(m_a))).$$

To find the exploitation rate (u) that produces maximum sustainable yield, we carried out simulations for u's ranging from 0 to 0.99 at an increment of 0.01. We assumed that the management strategy (fixed exploitation rate) was implemented without error. For each u, we carried out 100 simulations with maturity schedules that were constant and 100 simulations with maturity schedules that were random. The same set of random numbers was used for each exploitation rate and maturity schedule combination to ensure that any differences were not an artefact of the random number selection. We started each simulation at the equilibrium spawner biomass and age composition for the given exploitation rate and projected the population for 50 years.

Evaluation of Reference Points with the Simulation Model

We also used Monte Carlo simulations to examine the relationships between exploitation rates, catch and spawning escapement for each population, under the assumption of a fixed maturity schedule. For each projection, we calculated the minimum, maximum, mean, median, standard deviation, and 10^{th} through 90^{th} percentiles (increment of 10) of the catch and spawning escapement to summarize the projection. We then used the mean of these summary statistics for each exploitation rate to evaluate the effect of fishing at that rate on the population size and catch.

RESULTS

Comparison of the simulation results with variable and constant maturity schedules for the Margaree River show that variability in the maturity schedule has little effect on either the mean catch or spawning escapement (Figure 18), and hence little effect on the reference points. Standard deviations of the catch and spawning escapement are only slightly higher when stochastic variability in the maturity schedules is included in the simulations (Figure 18). Comparison of the percentiles of the catch (not shown) indicate that the distribution of the catch is only slightly more skewed when variability in the maturity schedule is included. Simulations with a range of $\alpha's$ and σ 's indicate that the variability around the SR model together with the high maximum reproductive rate have a much greater influence on spawning run size than does variability in the maturity schedule.

Summaries of the simulation results are shown for the Margaree River (Figure 19), Miramichi River (Figure 20), Mactaquac Headpond (Figure 21) and Gaspereau River (Figure 22). The fishing mortality rate that maximizes the mean catch, $F_{max.mean(C)}$, ranged from 0.53 for the Mactaquac Headpond to 0.91 for the Margaree River (Table 4). The fishing mortality rate that maximized the median catch, $F_{max.median(C)}$, ranged from 0.53 for the Mactaquac Headpond to 0.82 for the Margaree River. For all populations, the median catch curve is relatively flat over the middle part of the curve. The fishing mortality rates that produce 90% of the maximum of the median catch, $F_{90\%.median(C)}$, ranged between 0.31 for the Mactaquac Headpond to 0.46 for both the Gaspereau and Margaree River populations. These results show that exploitation rates can be reduced by nearly 20%

from the rate that maximizes the mean catch with only a 10% reduction in the mean yield of the fishery.

Francis (1993) proposed that a level of harvesting could be considered "safe" if it maintained the spawning stock biomass above 20% of its mean virgin level at least 90% of the time. The 10^{th} percentile of our simulation results can be used to find this level. Assuming a mean weight of 0.25 kg/fish, the exploitation rates that match this criterion are: 0.18 for the Margaree River, 0.42 for the Gaspereau River, 0.41 for the Mactaquac Headpond, and 0.27 for the Miramichi River. These rates are sensitive to the coefficient of variation assumed for the SR simulations (the Margaree River had the highest coefficient of variation, while the Gaspereau River had the lowest).

DISCUSSION

In this report we have estimated biological reference points for alewife fisheries in four rivers in the Maritime Provinces. The results show that while there are some differences in the biology of Gulf of St. Lawrence and Bay of Fundy alewife (primarily age-at-maturity), the differences are not sufficient to warrant different reference fishing mortality rates between the two regions. Annual variability in the maturity schedules has little effect on the mean catch and for a species such as alewife (with a high maximum reproductive rate and variability around the SR model), and does not need to be considered when selecting a reference F.

The current reference point for the Scotia-Fundy region (exploitation rates targeted not to exceed 65%) is based on the analysis of Crecco and Gibson (1990), and is approximately the mean of the MLE of u_{msy} for eight alewife populations (64%). In our study, F_{msy} (and the corresponding u_{msy}) is not well determined for any population, but was lower than this target for all populations except the Mactaquac Headpond. The exploitation rate that produces maximum sustainable yield is a function of α. In our meta-analysis of eight alewife stocks, the estimates of α were lower for populations with smaller confidence intervals than for those larger confidence intervals for α. This suggests that α is potentially overestimated for populations where it is not well determined. Additionally, time series bias (Walters 1985, Myers and Barrowman 1995) and measurement errors (Walters and Ludwig 1981, Ludwig and Walters 1981) cause α to be overestimated (although Kehler (2001) found that for the Ricker model, the direction of the bias depended on the range and distribution of the observed spawner abundance). When α is over-estimated, the exploitation rates that produce maximum sustainable yield or stock collapse are also over-estimated. Given that α is not well determined for any of the populations in our study, the resulting MLE of u_{msy} is probably not a good management target, given that most biases lead to its over-estimation.

Our results show that fishing mortality rates that maximize the expectation of the catch for these populations are lower than the MLE's for F_{msy}. $F_{max.E(C)}$ is therefore precautionary in the sense that it is less likely to lead to overexploitation of the populations. The simulation results show that even if the MLE's for α and R_0 are the "true" values, fishing at $F_{max.E(C)}$ will only have a small effect on either the mean or

median catch. Additionally, the simulation results suggest that an exploitation rate of about 40% will produce 90% the yield of fishing at the rate that produces the maximum yield (about 55 to 60% for populations other than the Mactaquac Headpond).

The Mactaquac Headpond population has the lowest maximum reproductive rate of any of the alewife populations for which we have data. The reference points for this population indicate that it should be fished at a lower rate as a result. However, we do not know why this population is less productive than others. Juvenile turbine mortality could potentially reduce recruitment in this population, although we do not have estimates of the rates of turbine mortality for this population. Alternatively, fish could be straying to other parts of the St. John River, or are not completing the migration as far as the Mactaquac Dam (as suggested by this analysis) or are being harvested in the lower river prior to reaching the dam (Jessop 1994). Most likely, all factors are acting concurrently, and it is also likely that fish are straying from downstream into the headpond (it was colonized from populations downstream). Therefore, while these analyses suggest that the population dynamics of this population differ substantially from other alewife populations, the analysis should not be considered conclusive until these issues are resolved.

Our simulation results suggest that fishing rates targeted at $F_{35\%}$ is probably a reasonable strategy for alewife in the Maritime Provinces. For all populations, this rate was less than F_{msy}, but still produced greater than 90% the maximum median catch. In this sense, it is precautionary if α is over-estimated in this study, but is not overly conservative because it produces a catch close to MSY if the estimated α's are close to their true values. This finding is similar to those of Clark (1991) and Mace and Sissenwine (1993). Clark found that $F_{35\%}$ would achieve at least 75% of the MSY yield when the SR relationship was unknown. In a meta-analysis of 91 SR datasets, Mace and Sissenwine found that $F_{30\%}$ was a reasonable threshold reference point for 80% of the populations included in the analysis, whereas Mace (1994) suggested that $F_{40\%}$ be adopted when the SR relationship is unknown. In our study, $F_{35\%}$ ranged between 0.47 (Margaree River) and 0.54 (Gaspereau River), with a corresponding average exploitation rate of 0.395.

Myers et al. (1994) suggested that the stock size corresponding to 50% the maximum average recruitment (the K parameter in the Beverton-Holt SR model) could be interpreted as a minimum biomass level at which recruitment to a fish stock is seriously reduced. For these populations this threshold is well below SSB_{msy} or $SSB_{20\%}$. For example, for the Gaspereau River population, these values are 16.2t, 85.8t and 109.3t for K, SSB_{msy}, and $SSB_{20\%}$ respectively. Myers et al. warn that for populations with an estimated slope at the origin that is high, the use of K as a threshold could produce population sizes that are very low. For the Gaspereau River, only one observed spawner abundance is below K, although all observed spawner abundances are below SSB_{msy}, and harvest rates at times have exceeded 85%. As discussed earlier, many of the biases in the estimation of α lead to its overestimation and hence to an underestimation of K. In these instances, biomass thresholds based on a percentage of virgin biomass may be preferable, although the selection of an appropriate percentage remains problematic (Myers et al.

1994). The alewife populations in this study have been heavily exploited. For the Gaspereau River, all predicted spawner abundances are below $SSB_{20\%}$ and all but two predicted spawner abundances are below $SSB_{20\%}$ for the Margaree River. The Mactaquac Headpond appears to be at low levels relative to the carrying capacity of alewife habitat (Gibson and Myers in press[2]), and reasonable estimates of K cannot be estimated from the stock specific data for the Miramichi River. Given these issues, the biomass thresholds presented herein should be treated as preliminary until further data at higher spawner abundances is collected for each population. However, the estimated carrying capacities of habitat for these four populations are lower than the mean of the empirical Bayes prior distribution for carrying capacity for alewife at the species level, suggesting that we are not overestimating the biomass thresholds for these populations. If this is true, these populations have been at or below $SSB_{20\%}$ during the period for which we have data.

Spawner-recruit model selection affects the resulting reference point estimates. Gibson and Myers (in press[2]) found that the Beverton-Holt model produces better fits to alewife SR data than the Ricker model, and were unable to find evidence of depensation in alewife SR data. The Beverton-Holt model generally produces higher estimates of the slope at the origin than the Ricker model, and is not a precautionary selection as a result (Myers et al. 1999, Myers et al. 2002). Barrowman and Myers (2000) present an alternative SR model, the hockey-stick model, based on territoriality in the pre-recruit life stages (applicable for salmon). This model also produces estimates of the slope at the origin that are lower than those from the Beverton-Holt model. The hockey stick model can be used for estimating threshold biomass estimates (Bradford et al. 2000) because one of the parameters, S^*, is the threshold spawner biomass at which recruitment begins to decline. While not analyzed in detail here (alewife are not territorial), this model produces threshold biomass estimates (S^*) that are slightly higher than K for these populations. SSB_{msy} equals S^* when estimated using the hockey stick model, producing an estimate 26.1t for SSB_{msy} (at $u = 0.85$) for the Gaspereau River (in comparison with 85.8t, at $u = 0.63$, from the Beverton-Holt model). This example shows that model selection not only has consequences for limit fishing mortality rates (Barrowman and Myers (2000), but for biomass thresholds as well.

Understanding the distributional properties of biological reference points and the precision of their estimates is crucial as the use of reference points becomes more prevalent in fisheries management (Caddy and McGarvey 1996, Overholtz 1999). Overholz (1999) presented a bootstrap method that could be used to assess the precision of reference points and cumulative probability distributions that can be used for inference about the resulting estimates. In our study, we assessed the precision of the production model reference point estimates using profile likelihoods. For reference points with profile likelihoods that are ramped, probabilistic statements cannot be made without placing bounds on the range of possible reference point values. When calculating the fishing mortality rate that maximized the expectation of the catch, we used the random effects distribution from a mixed effects model for the SR parameters to obtain these bounds. Additionally, the resulting distributions for the SR parameters can be used to assess the plausibility of the estimates resulting from fits to individual stocks, and to

obtain empirical Bayes estimates for the model parameters for individual populations (Myers et al. 1999, Myers et al. 2001).

Currently, a formal definition of risk has not been adopted for alewife in the Maritime Provinces. Francis (1993) suggested that a level of harvesting could be considered "safe" if it maintained the spawning stock biomass above 20% its mean virgin level at least 90% of the time. $F_{35\%}$ estimated in our analyses corresponds roughly with this definition for the Gaspereau River and Mactaquac Headpond population simulations, but did not meet this objective in the Margaree and Miramichi River simulations. When estimated using a simulation model, the level of harvesting that is considered "safe" depends largely on the amount of random variability introduced during the simulations. If the coefficient of variation (CV) estimated for the SR models is greater (due to measurement error) than the true variability in the SR process, the resulting "safe" level of fishing will be underestimated. The estimates of a "safe" level of harvesting for the Margaree and Miramichi rivers are lower than any of the other reference points for these populations and their CV is higher than for the Scotia-Fundy populations. Measurement error is not separated from process error in our models, and it is therefore probable that the CV is overestimated for the Gulf Region stocks. We would therefore not recommend reducing the reference point below $F_{35\%}$ on the basis of this analysis until accuracy of the CV estimates is evaluated.

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Table 1. Statistical models used to reconstruct the size and run composition of the alewife populations in the Maritime Provinces. Notation is explained in the text.

	Populations		
	Gaspereau River	Margaree and Miramichi Rivers	Mactaquac Headpond
Dynamics:	$N_{t,s,a,0} = R_{t-a+3}\upsilon_s m_{s,a}\exp\left(-M^{juv}(a-3)\right)$	$N_{t,a,p} = N_{t-p,a-p,0}\exp\left(-\left(\sum_{k=t-p+1}^{t} F_k + M^{adult}p\right)\right)$	$N_{t,s,a,p} = N_{t-p,s,a-p,0}\exp\left(-\left(\sum_{k=t-p+1}^{t} F_k + M^{adult}p\right)\right)$
	$C_{t,s,a,p} = N_{t,s,a,p}u_t$	$C_{t,a,p} = N_{t,a,p}u_t$	$C_{t,s,a,p} = N_{t,s,a,p}u_t$
	$C_t = \sum_s\sum_a\sum_p\left(N_{t,s,a,p}u_t\right)$	$C_t = \sum_a\sum_p\left(N_{t,a,p}u_t\right)$	$C_t = \sum_s\sum_a\sum_p\left(N_{t,s,a,p}u_t\right)$
	$E_{t,s,a,p} = N_{t,s,a,p}(1-u_t)$	$E_{t,a,p} = N_{t,a,p}(1-u_t)$	$E_{t,s,a,p} = N_{t,s,a,p}(1-u_t)$
	$SSB_t = \sum_s\sum_a\sum_p\left(E_{t,s,a,p}w_a\right)$	$SSB_t = \sum_a\sum_p\left(E_{t,a,p}w_a\right)$	$SSB_t = \sum_s\sum_a\sum_p\left(E_{t,s,a,p}w_a\right)$
	$R_t = \sum_s\sum_{a=3}^{6}\left(N_{t+a,s,a,0}/\exp\left(-M^{juv}(a-3)\right)\right)$	$R_t = \sum_{a=2}^{6}\left(N_{t+a,a,0}/\exp\left(-M^{juv}(a-3)\right)\right)$	$R_t = \sum_s\sum_{a=3}^{6}\left(N_{t+a,s,a,0}/\exp\left(-M^{juv}(a-3)\right)\right)$
Log Likelihoods (non-constant portions):	$\ell_{catch} = -\sum_t\left(\ln C_t^{obs} - \ln C_t\right)^2$	$\ell_{catch} = -\sum_t\left(\ln C_t^{obs} - \ln C_t\right)^2$	$\ell_{catch} = -\sum_t\left(\ln C_t^{obs} - \ln C_t\right)^2$
	$\ell_{composition} = -\sum_t\sum_s\sum_a\sum_p n_{t,s,a,p}^{obs}\ln p_{t,s,a,p}$	$\ell_{composition} = -\sum_t\sum_a\sum_p n_{t,a,p}^{obs}\ln p_{t,a,p}$	$\ell_{composition} = -\sum_t\sum_s\sum_a\sum_p n_{t,s,a,p}^{obs}\ln p_{t,s,a,p}$
	$\ell_{escapement} = -\sum_t\left(\ln E_t^{obs} - \ln E_t\right)^2$		$\ell_{escapement} = -\sum_t\left(\ln E_t^{obs} - \ln E_t\right)^2$
Objective Functions:	$O.B.V. = -(\lambda_1\ell_{composition} + \lambda_2\ell_{catch} + \lambda_3\ell_{escapement})$	$O.B.V. = -(\lambda_1\ell_{composition} + \lambda_2\ell_{catch})$	$O.B.V. = -(\lambda_1\ell_{composition} + \lambda_2\ell_{catch} + \lambda_3\ell_{escapement})$
Estimated Parameters:	R_{t-a+3} (20 parameters)	$N_{t,a,0}$ (Margaree: 90 parameters)	$N_{t,s,a,0}$ (216 parameters)
	$m_{s,a}$ (6 parameters)	(Miramichi: 76 parameters)	u_t (27 parameters)
	M^{adult} (1 parameter)	u_t (Margaree: 18 parameters)	M^{adult} (1 parameter)
		(Miramichi: 19 parameters)	
		M^{adult} (1 parameter)	

Table 2. Datasets used for the spawning run reconstructions of four alewife populations in the Maritime Provinces.

	Population			
Data Type	Gaspereau River	Margaree River	Miramichi River	Mactaquac Headpond
Catch:	1982 to 2001	•1983 to 2000	1982 to 2000	1973 to 1999
Escapement Counts:	1982 to 1984 1995 1997 to 2001	not available	not available	1973 to 1999
Run Compostion:	1982 to 1984 1997 to 2001	1983 to 2000 (age and p.s. only)	1982 to 2000 (age and p.s. only)	1973 to 1999
Larval Index:	not available	1983 to 1985 1989 to 1991 1993 to 2000	not available	not available

Table 3. Parameter estimates obtained from the assessment and SR models that were used as input parameters for the simulation models and to calculate reference points. Numbers in brackets are standard errors.

	Population			
Parameter:	Gaspereau River	Margaree River	Miramichi River	Mactaquac Headpond
SR Model:				
α	96.10	73.88	>10,000[1]	32.79
R_0	1,563,665	6,915,954	7,400,447	2,296,051
K	16,217	93,603	<1	36,888
σ	0.42	1.26	0.94	0.65
Assessment Model:				
M^{adult}	0.53 (0.05)	0.44 (0.01)	0.49 (1.02)	0.25[2] (0.08)
m_2	<0.01	<0.01	<0.01	<0.01
m_3	<0.01	0.52	0.37	0.06
m_4	0.53	0.97	0.91	0.49
m_5	0.98	0.94	0.83	0.93
m_6	1.00	1.00	1.00	1.00
			[1]73.88 used in simulations	[2]0.53 used in simulations and BRP calculations

Table 4. Biological reference points for the Margaree River, Gaspereau River, Miramichi River and Mactaquac Headpond alewife populations. Values in brackets are the corresponding exploitation rates. Definitions of the reference points are explained in the text.

Theoretical Basis	Reference Point	Margaree River	Gaspereau River	Miramichi River	Mactaquac Headpond
Yield per Recruit	$F_{0.1}$	0.61 (0.50)	0.86 (0.58)	0.76 (0.53)	0.76 (0.54)
	F_{max}	>3.0 (>0.99)	>3.0 (>0.99)	>3.0 (>0.99)	>3.0 (>0.99)
Spawner per Recruit	$F_{35\%}$	0.47 (0.37)	0.54 (0.42)	0.50 (0.39)	0.51 (0.40)
	$F_{25\%}$	0.67 (0.49)	0.77 (0.54)	0.71 (0.51)	0.72 (0.52)
	F_{med}	0.86 (0.58)	1.12 (0.67)	0.79 (0.54)	0.42 (0.34)
	F_{high}	1.88 (0.85)	1.98 (0.86)	1.61 (0.80)	1.03 (0.64)
	F_{low}	0.00 (0.00)	0.93 (0.60)	0.00 (0.00)	0.00 (0.00)
Production Model	F_{col}	2.72 (0.93)	2.60 (0.92)	4.61 (>0.99)	1.82 (0.84)
	F_{msy}	0.98 (0.62)	1.01 (0.63)	4.61 (>0.99)	0.68 (0.41)
	SSB_{msy}	622.3 t	85.8 t	14.1 t	123.0 t
	$SSB_{20\%}$	883.8 t	109.3 t	865.3 t	112.5 t
Decision Theoretic	F_{mmy}	0.82 (0.56)	0.78 (0.55)	0.87 (0.58)	0.76 (0.53)
	$F_{max.E(C)}$	0.75 (0.53)	0.82 (0.56)	0.75 (0.53)	0.75 (0.53)
Simulation Based	$F_{max.mean(C)}$	0.78 (0.55)	0.94 (0.61)	0.86 (0.58)	0.53 (0.41)
	$F_{max.median(C)}$	0.71 (0.51)	0.91 (0.60)	0.84 (0.57)	0.53 (0.41)
	$F_{90\%.mean(C)}$	0.44 (0.36)	0.52 (0.41)	0.47 (0.38)	0.33 (0.28)
	$F_{90\%.median(C)}$	0.37 (0.31)	0.51 (0.40)	0.43 (0.35)	0.31 (0.27)

Table 5. A comparison of the exploitation rates that maximize the expectation of the catch for four alewife populations based on four methods of calculating the joint probability density for α and R_0. The estimates labeled "uniform bounded prior" are calculated assuming no information other than the upper and lower bounds for α and R_0 is available. The "prior distributions only" estimates are calculated using the probability density calculated from the mixed model random effects distributions for α and R_0. The "joint posterior distribution" is calculated using the likelihood surface and the random effects distributions. The fishing mortality rate that produces maximum sustainable yield based on the maximum likelihood estimates of SR parameters is included for comparison.

Population	Based on Stock Specific Information Only		Information From Other Populations Included		
	$Fmsy$ M.L.E.	Likelihood Surface Only	Uniform Bounded Prior	Prior Distributions Only	Joint Posterior Distribution
Gaspereau River	0.63	0.54	0.49	0.56	0.56
Maragree River	0.62	0.45	0.49	0.53	0.53
Miramichi River	<0.99	0.54	0.49	0.53	0.53
Mactaquac Headpond	0.49	0.21	0.46	0.53	0.53

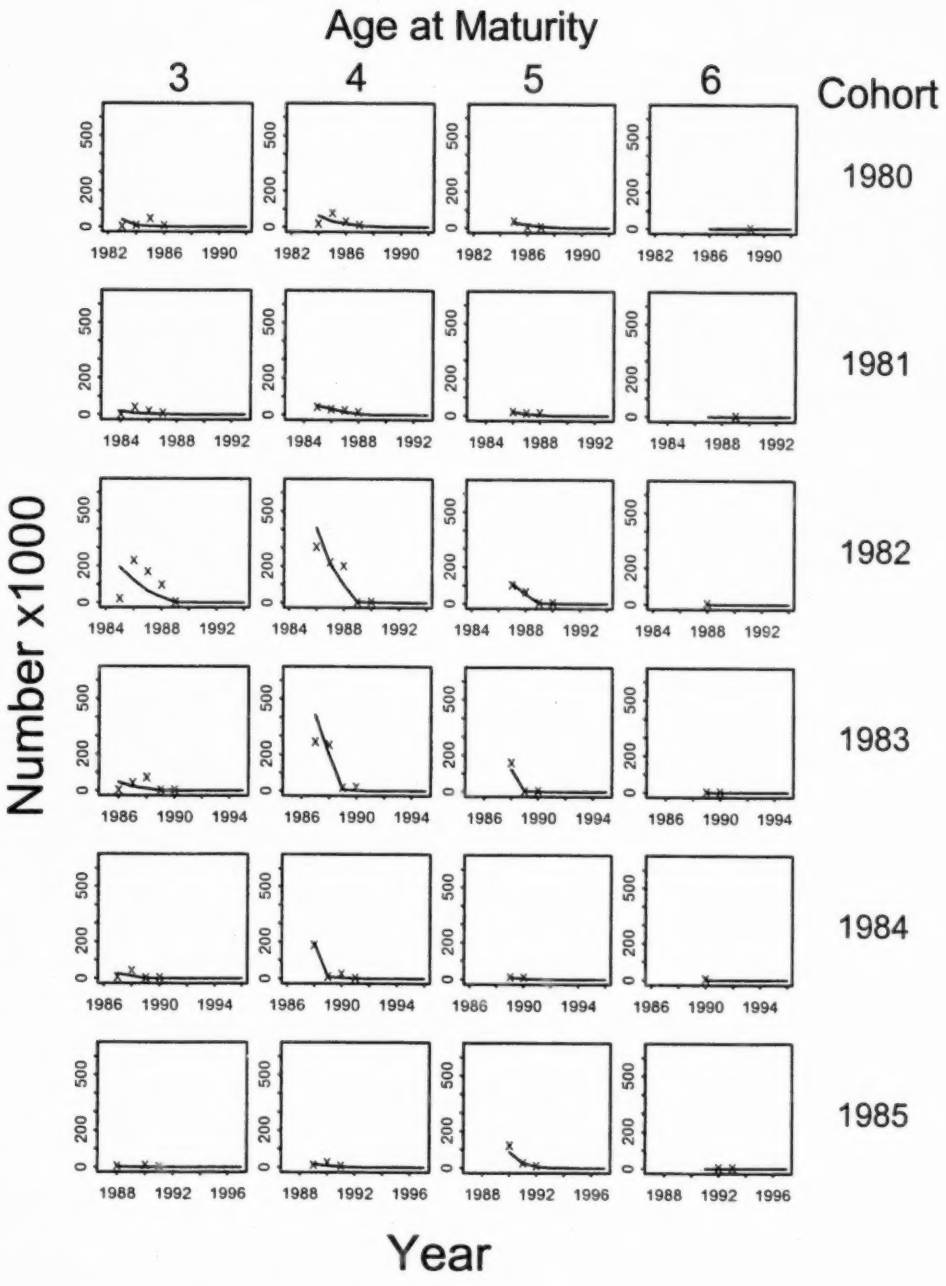

Figure 1. Part of the observed (x's) and predicted (lines) spawning escapement arrays for the Mactaquac Headpond alewife population (females only). Escapements are partitioned by cohort year (right column) and age at maturity (labels at the top). The year (bottom labels) is the year of capture.

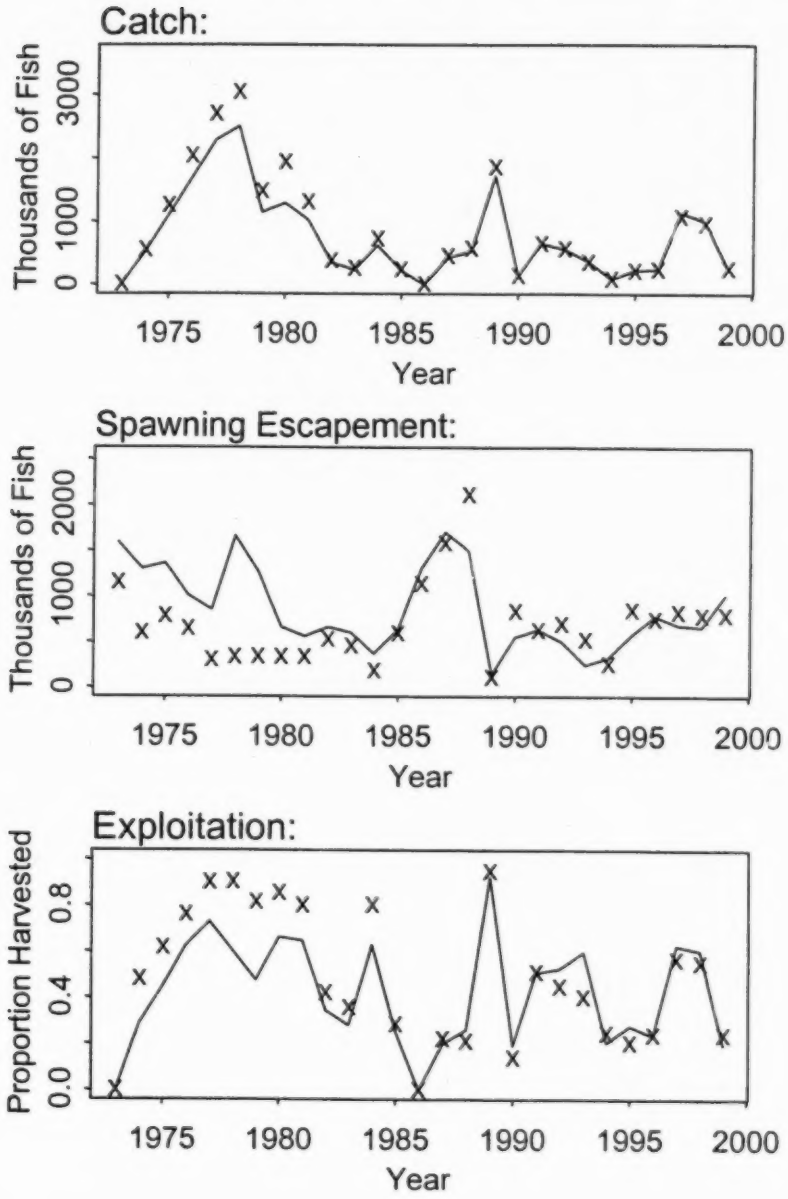

Figure 2. Observed (x's) and predicted (solid lines) catches, spawning escapements and exploitation rates for the Mactaquac Headpond alewife population.

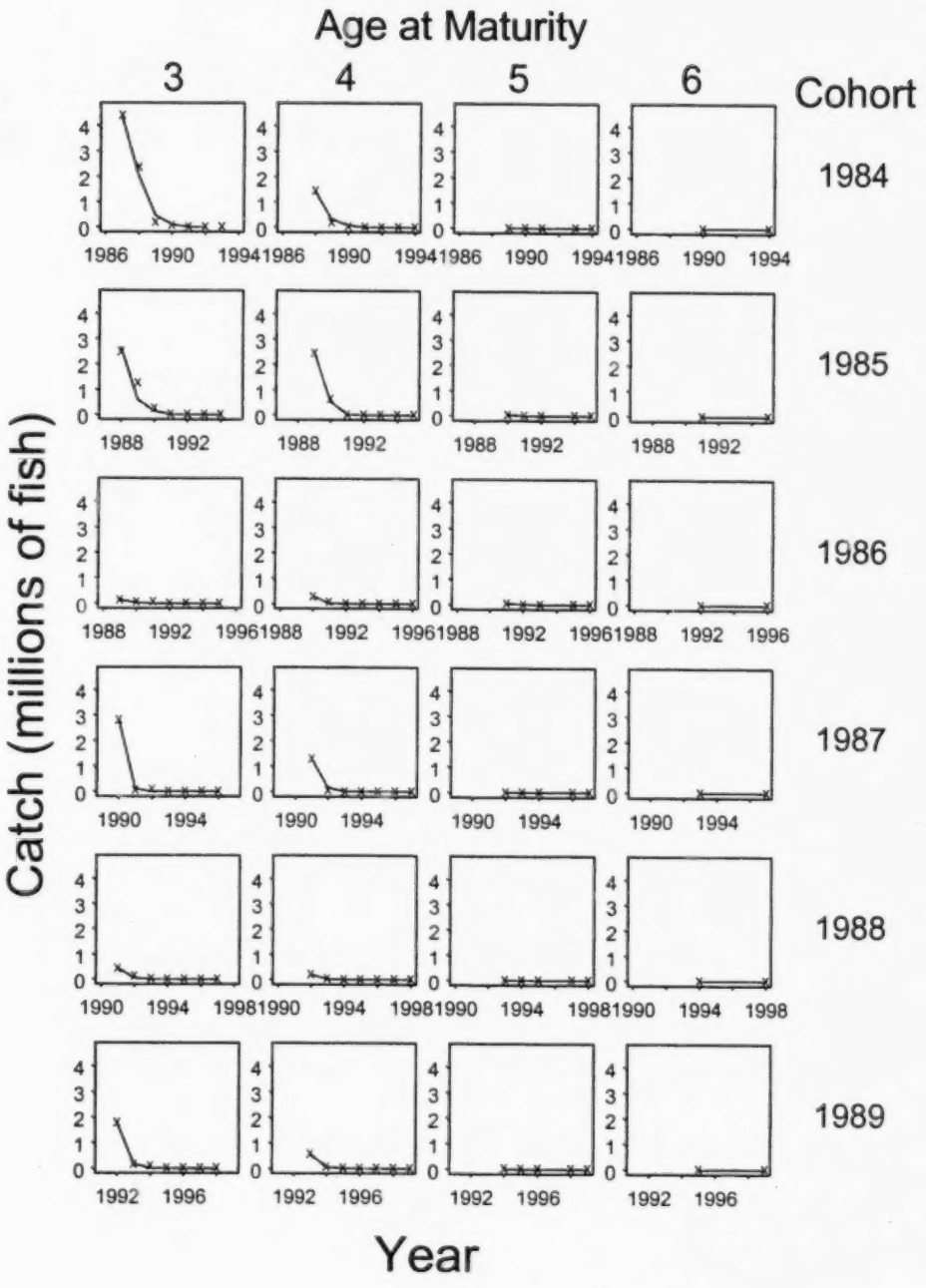

Figure 3. Part of the observed (x's) and predicted (lines) spawning escapement arrays for the Margaree River alewife population (sexes combined). Escapements are partitioned by cohort year (right column) and age at maturity (labels at the top). The year (bottom labels) is the year of capture.

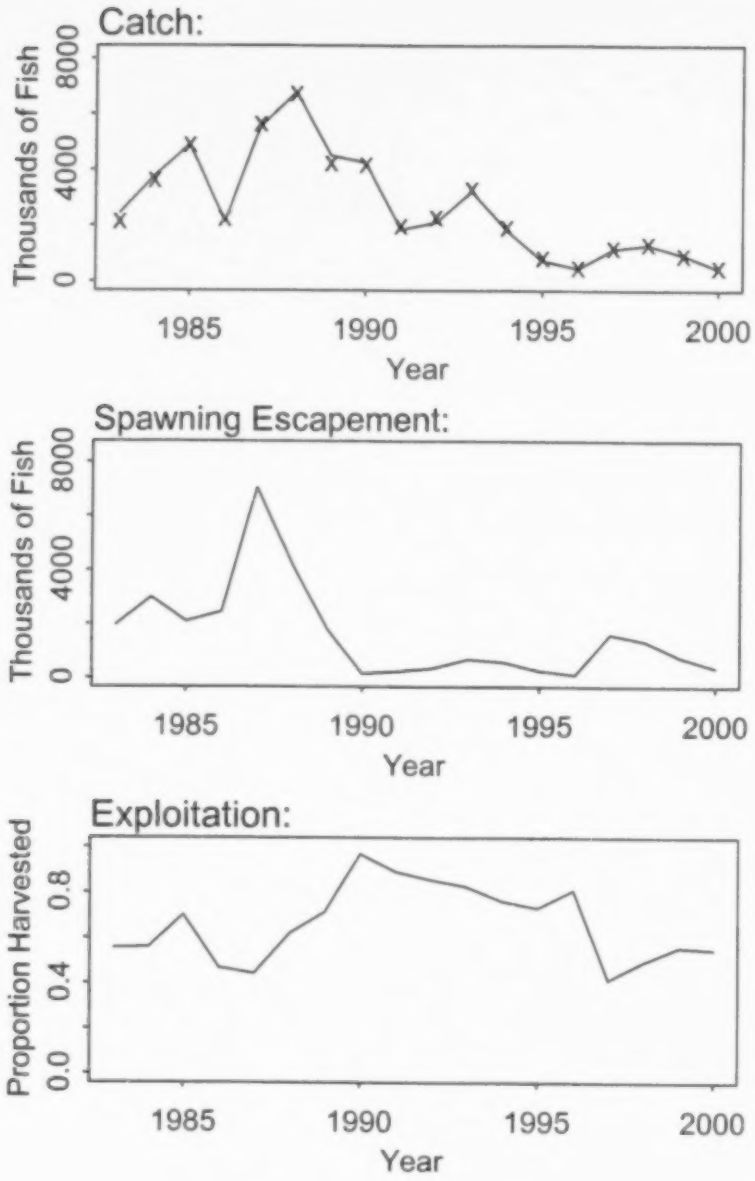

Figure 4. Observed (x's) and predicted (solid lines) catches, and predicted spawning escapements and exploitation rates for the Margaree River alewife population.

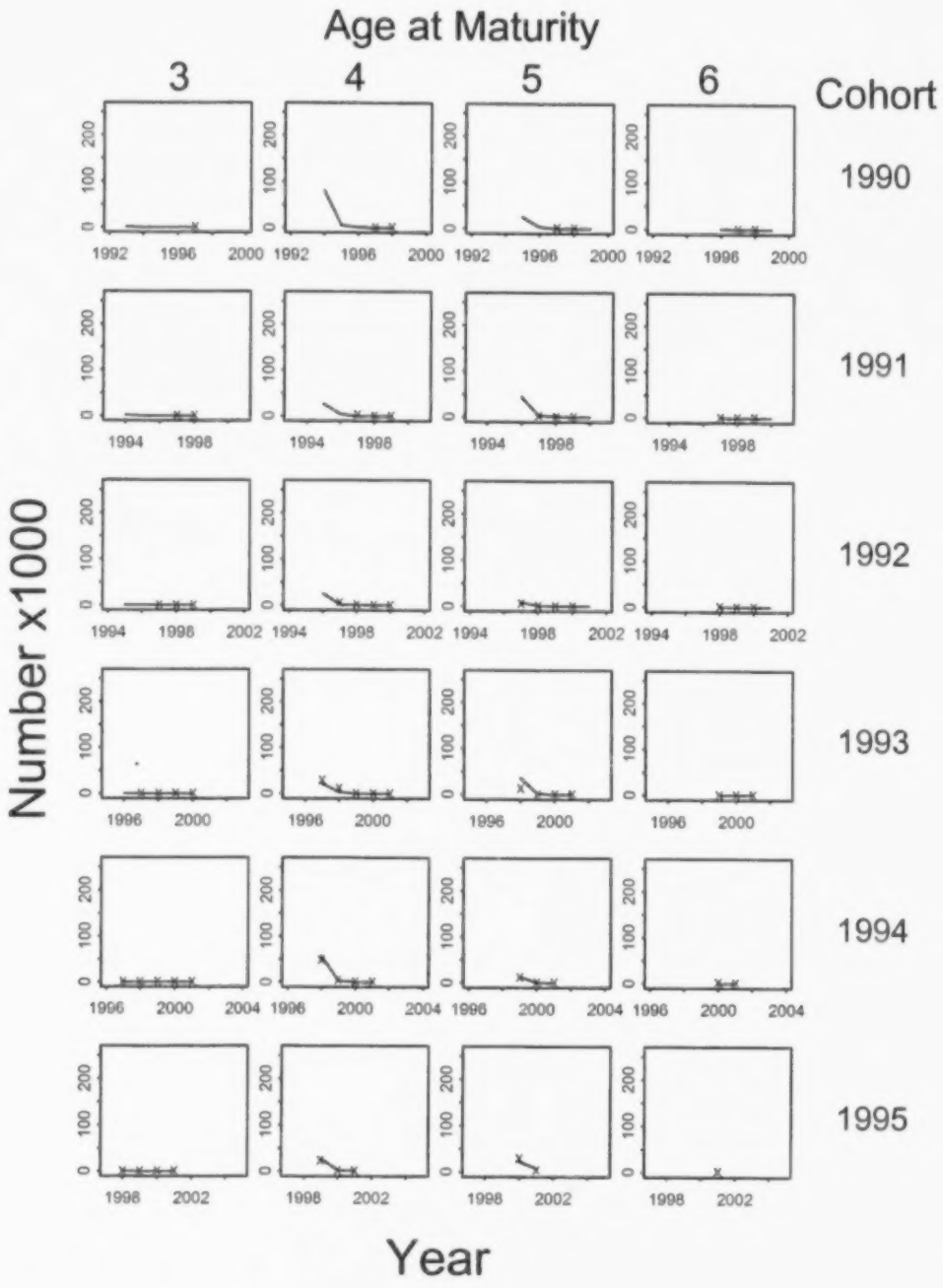

Figure 5. Part of the observed (x's) and predicted (lines) spawning escapement arrays for the Gaspereau River alewife population (females only). Escapements are partitioned by cohort year (right column) and age at maturity (labels at the top). The year (bottom labels) is the year of capture.

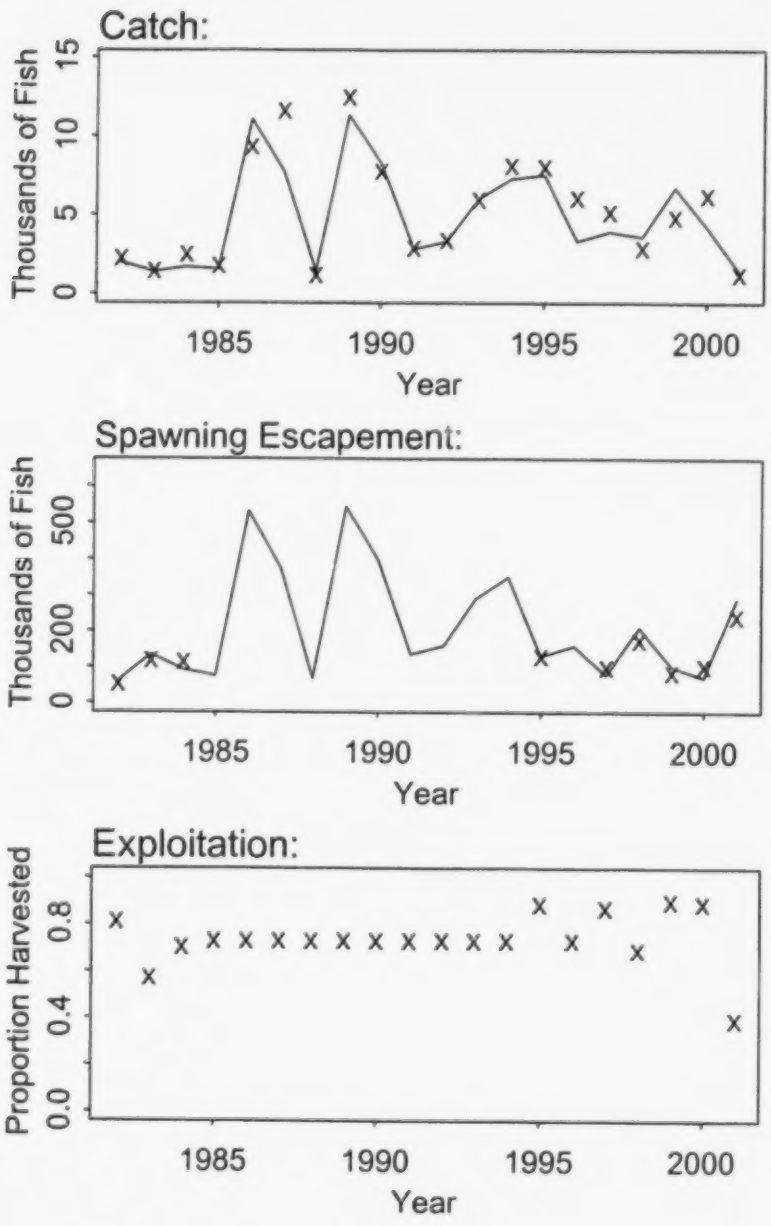

Figure 6. Observed (x's) and predicted (solid lines) catches and spawning escapements for the Gaspereau River alewife population. The exploitation rates were assumed known in the assessment model for this population.

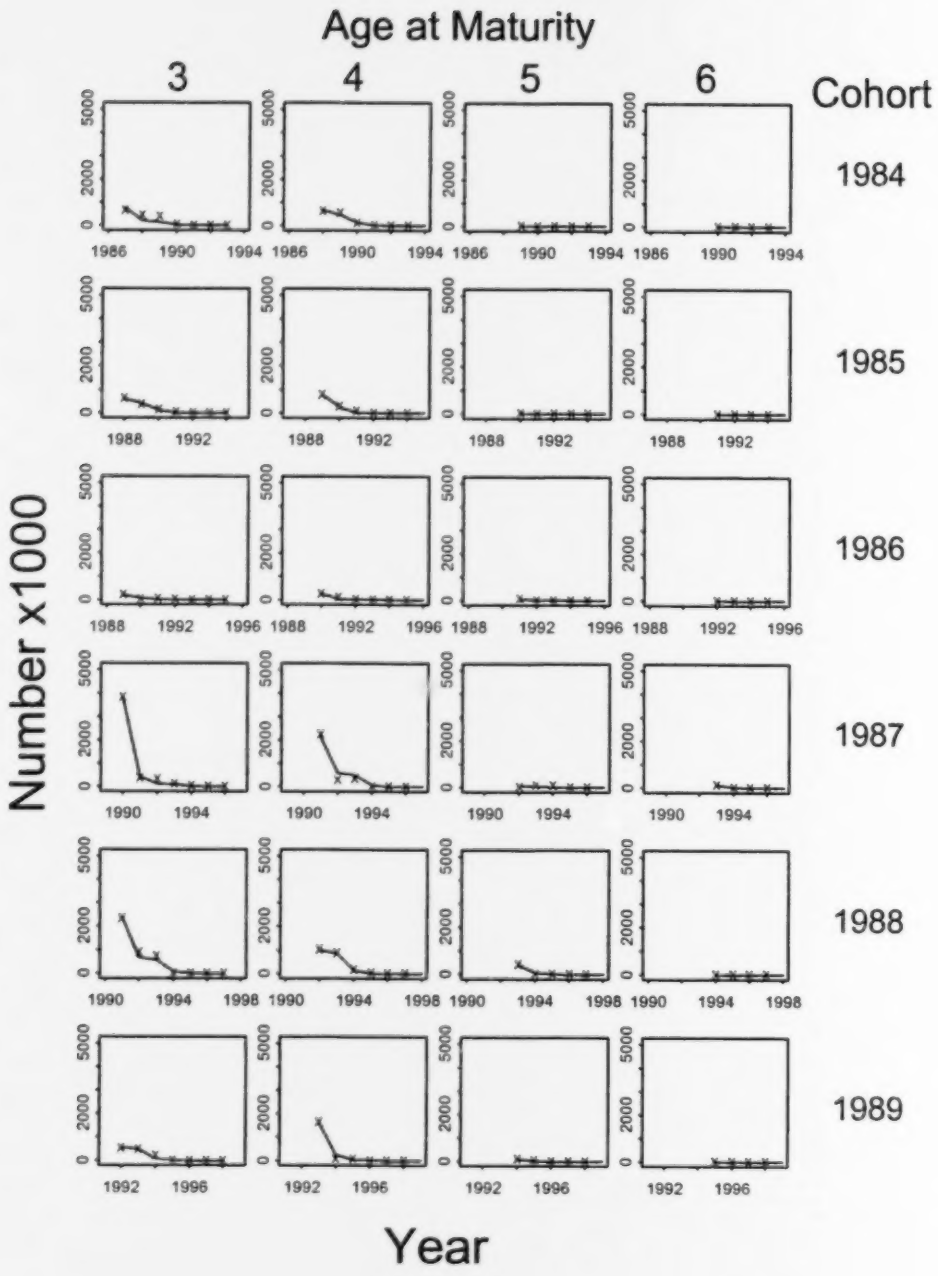

Figure 7. Part of the observed (x's) and predicted (lines) spawning escapement arrays for the Miramichi River alewife population (sexes combined). Escapements are partitioned by cohort year (right column) and age at maturity (labels at the top). The year (bottom labels) is the year of capture.

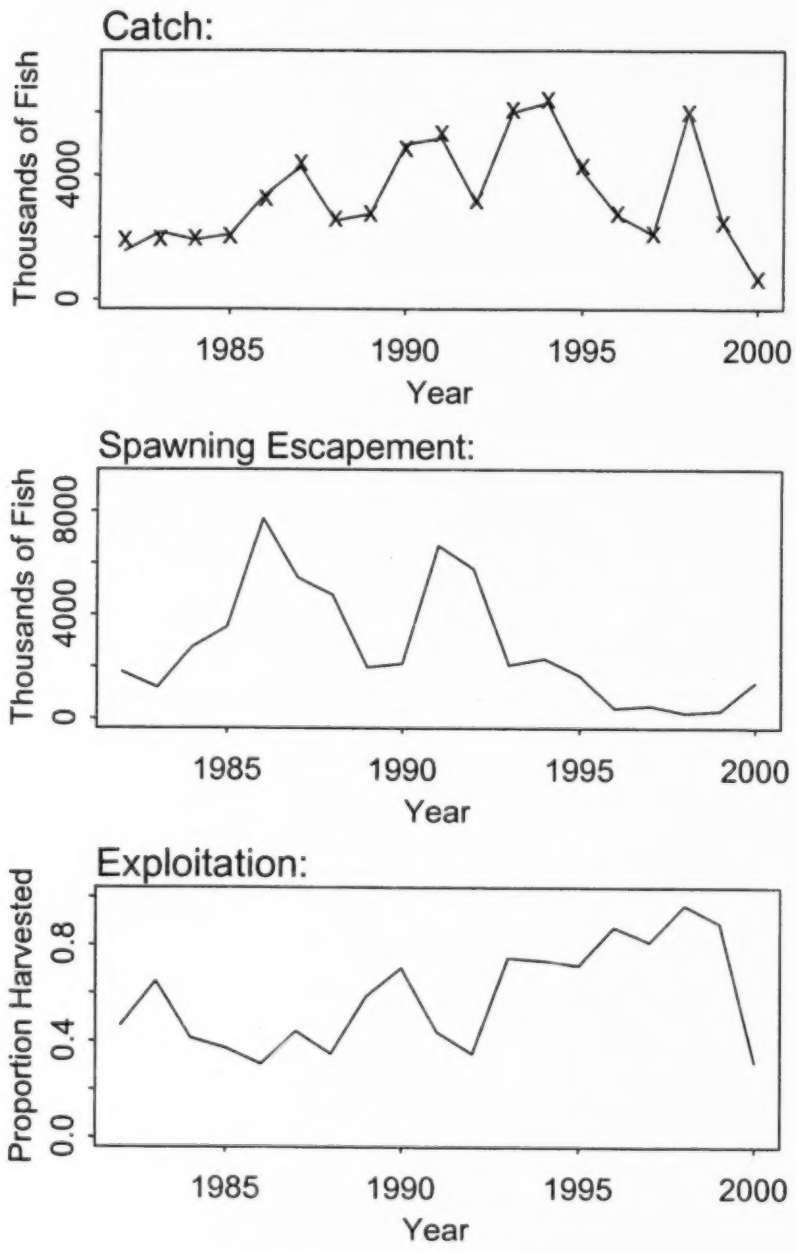

Figure 8. Observed (x's) and predicted (solid lines) catches, and predicted spawning escapements and exploitation rates for the Miramichi River alewife population.

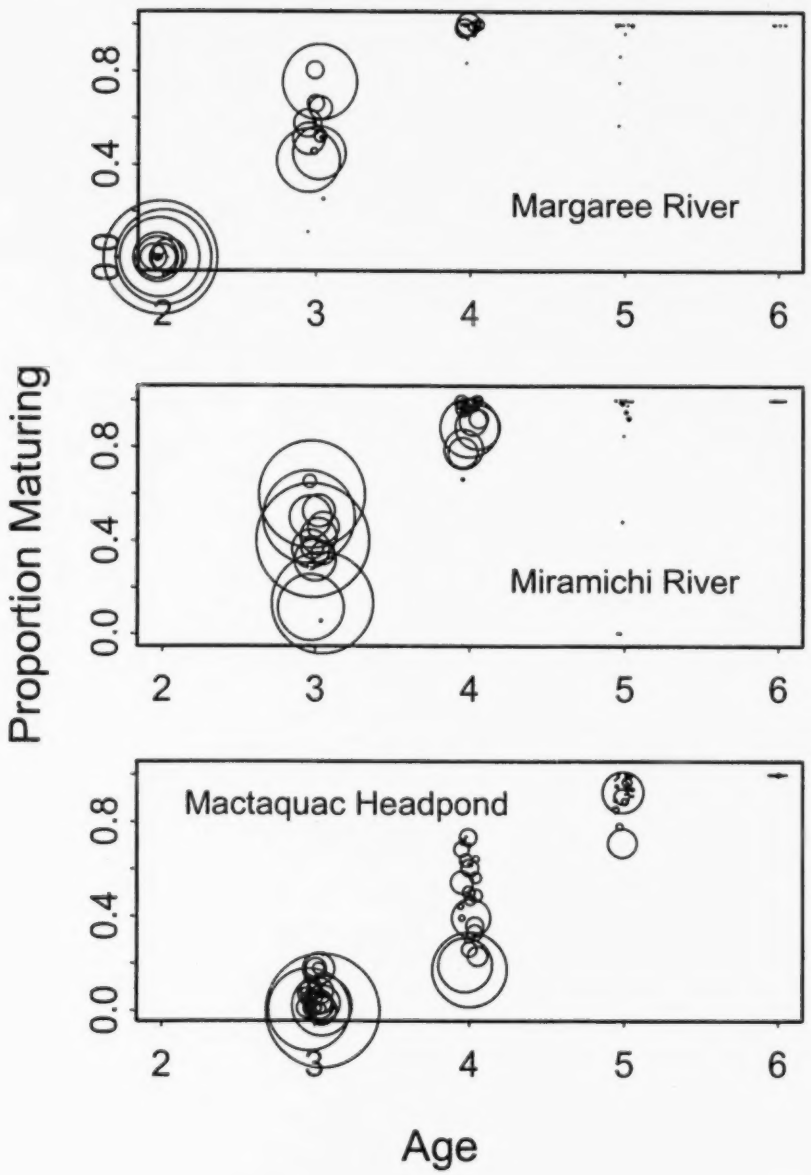

Figure 9. Variability in the age at maturity for the Margaree River, Miramichi River and Mactaquac Headpond alewife populations. Each point (or circle) represents the proportion of fish within a cohort that were alive at a given age and matured at that age. The size of the circle is proportional to the number of immature fish in the cohort at that age. Points are jittered slightly to facilitate display.

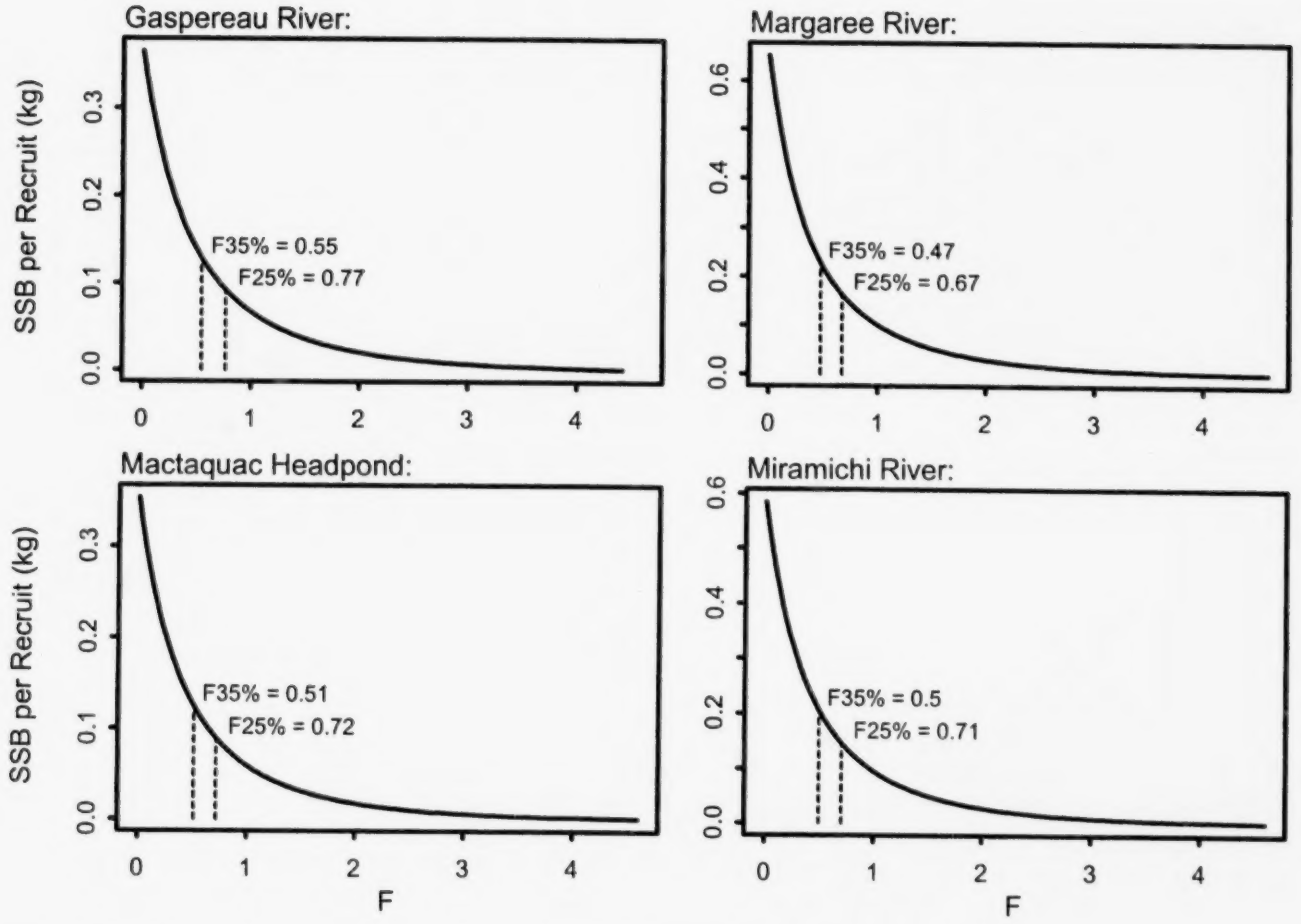

Figure 10. The relationship between the instantaneous rate of fishing mortality (F) and spawning biomass per recruit for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations.

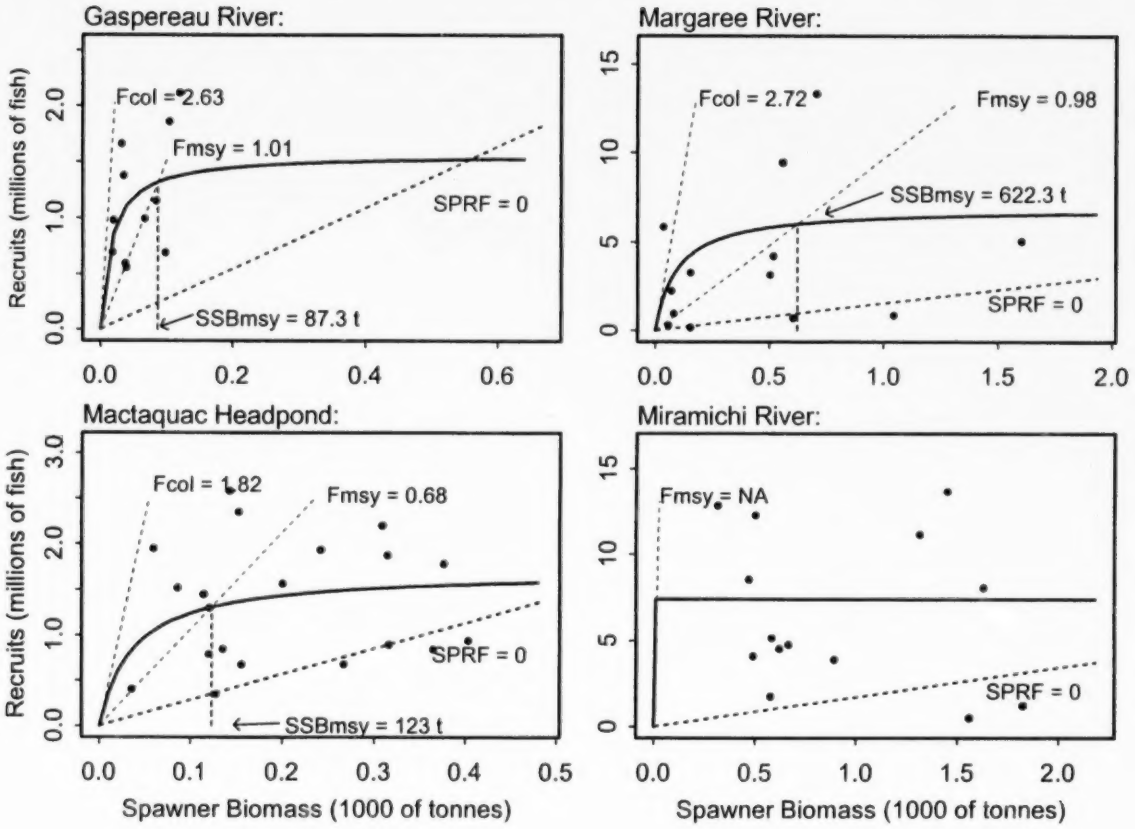

Figure 11. Beverton-Holt spawner-recruit models (solid line) and production model reference points for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations. The dashed line labelled "SPRF0" is the replacement line in the absence of fishing mortality.

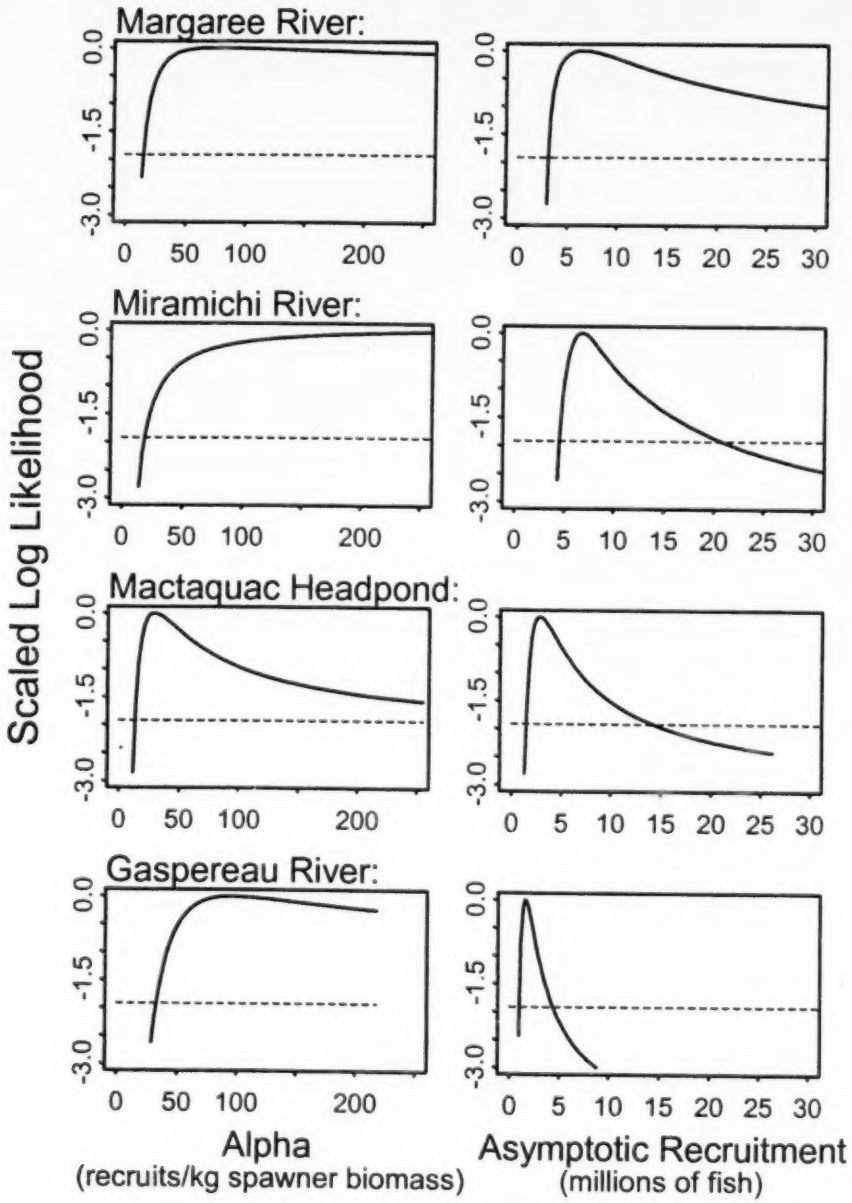

Figure 12. Profile log likelihoods (solids lines) for alpha (left column) and the asymptotic recruitment level (right column) for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations. The log likelihoods are standardized to a maximum of 0 by subtracting the maximum log likelihood from each estimate. The intersections between the dotted lines and the profile likelihoods show a likelihood ratio based 95% confidence intervals for each parameter. Upper and lower bounds cannot be determined for some populations.

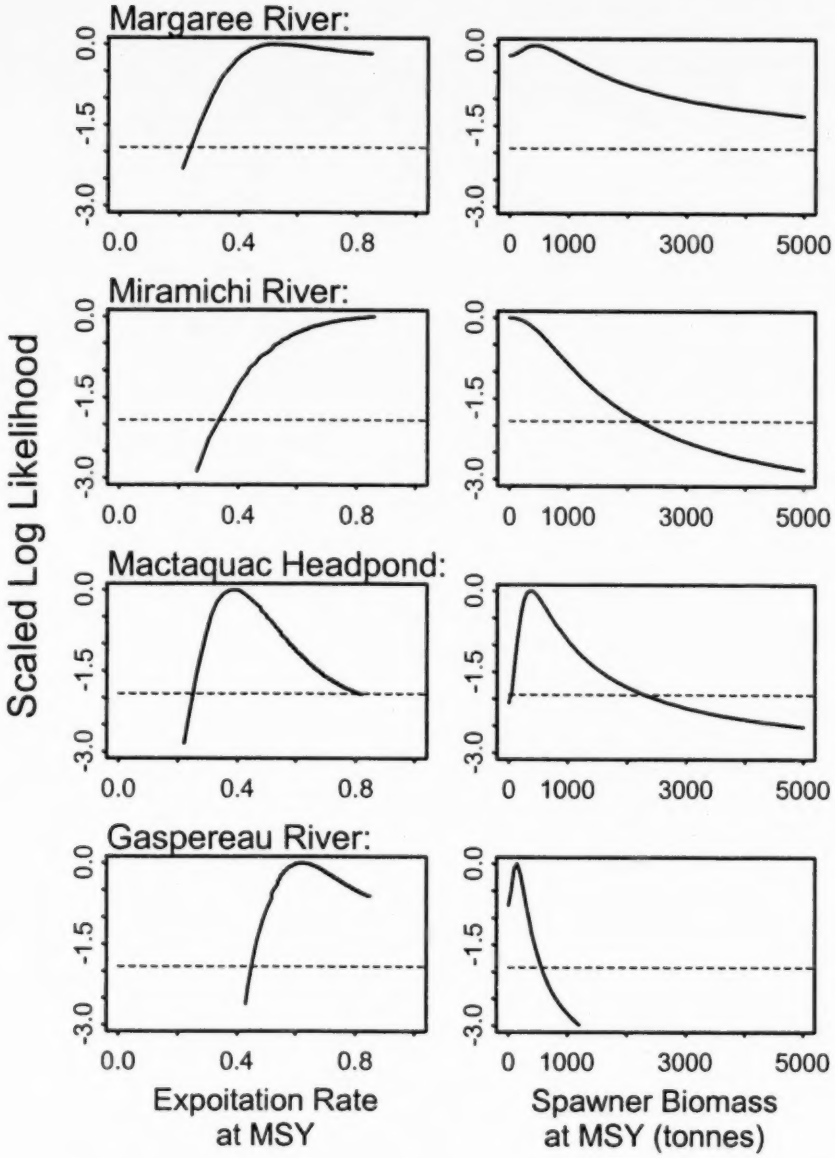

Figure 13. Profile log likelihoods (solids lines) for the exploitation rate that produces maximum sustainable yield (left column) and the spawning biomass that produces maximum sustainable yield (right column) for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations. The log likelihoods are standardized to a maximum of 0 by subtracting the maximum log likelihood from each estimate. The intersections between the dotted lines and the profile likelihoods show a likelihood ratio based 95% confidence intervals for each parameter. Upper and lower bounds cannot be determined for all populations.

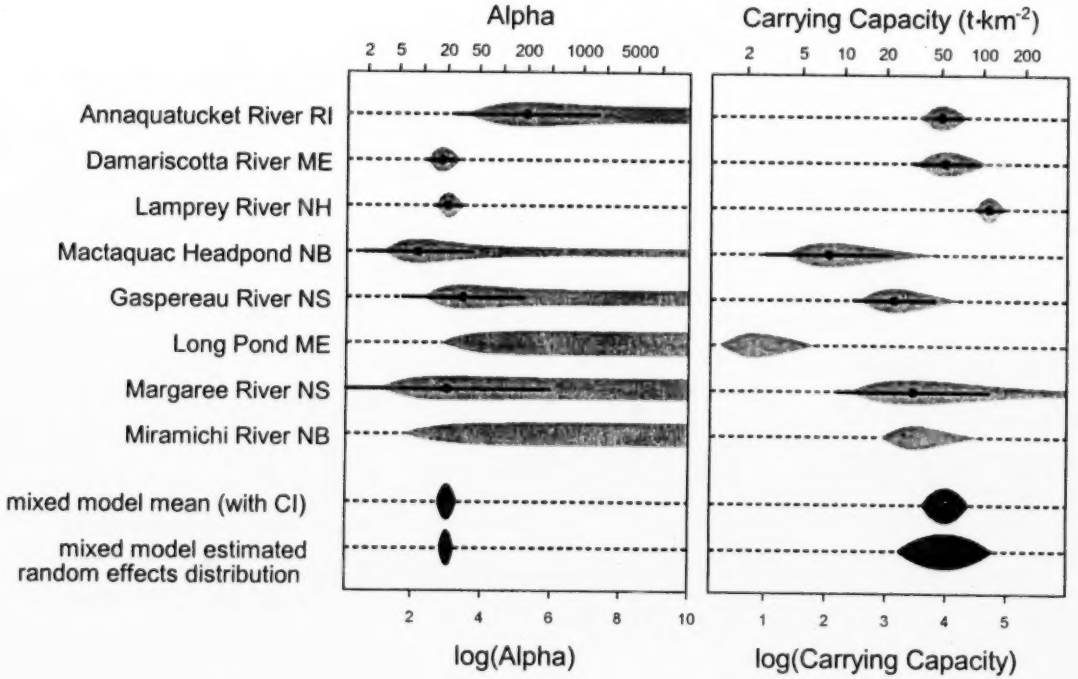

Figure 14. A meta-analytic summary of the maximum lifetime reproductive rate (alpha) and the habitat carrying capacity for eight alewife populations (modified from Gibson and Myers in press[2]). The light grey shaded regions are individual fits that depict the profile likelihood for each parameter, truncated to show the 95% confidence interval. The profile is used to gauge the relative plausibility of different values (wider is more plausible). The black dot is the maximum likelihood estimate for each parameter. Convergence of the nonlinear least squares algorithm was not obtained for the Miramichi and Long Pond populations. Where convergence was obtained, approximate asymptotic 95% confidence intervals are shown (black line). The dark grey shaded regions show summaries of the mixed model results. The "mixed model mean" represents the estimated mean of the logarithm of each parameter with a 95% confidence interval. The "mixed model estimated random effects distribution" is the normal distribution for the logarithm of each parameter based on its mean and variance estimated with the mixed effects model.

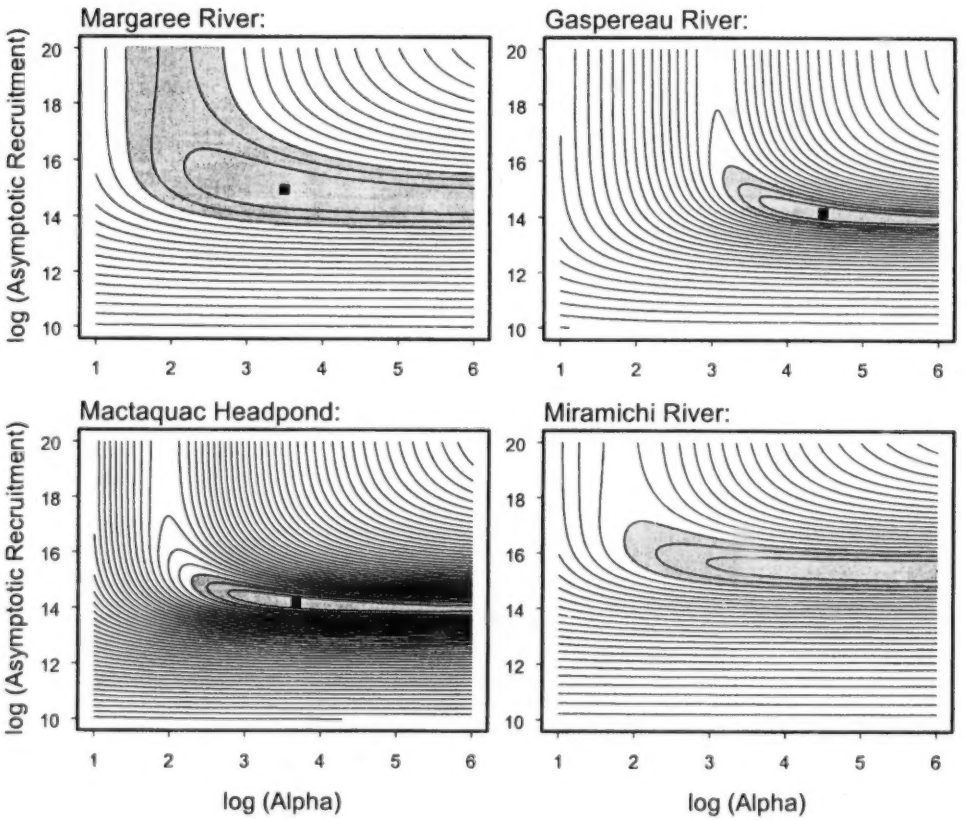

Figure 15. Contour plots showing the joint log likelihood surface for alpha and the asymptotic recruitment level for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations. The black square indicates the point at which the log likelihood is maximized. The contour interval is -1 moving away from this point. The grey shaded region shows the likelihood ratio based 95% confidence region for the parameters.

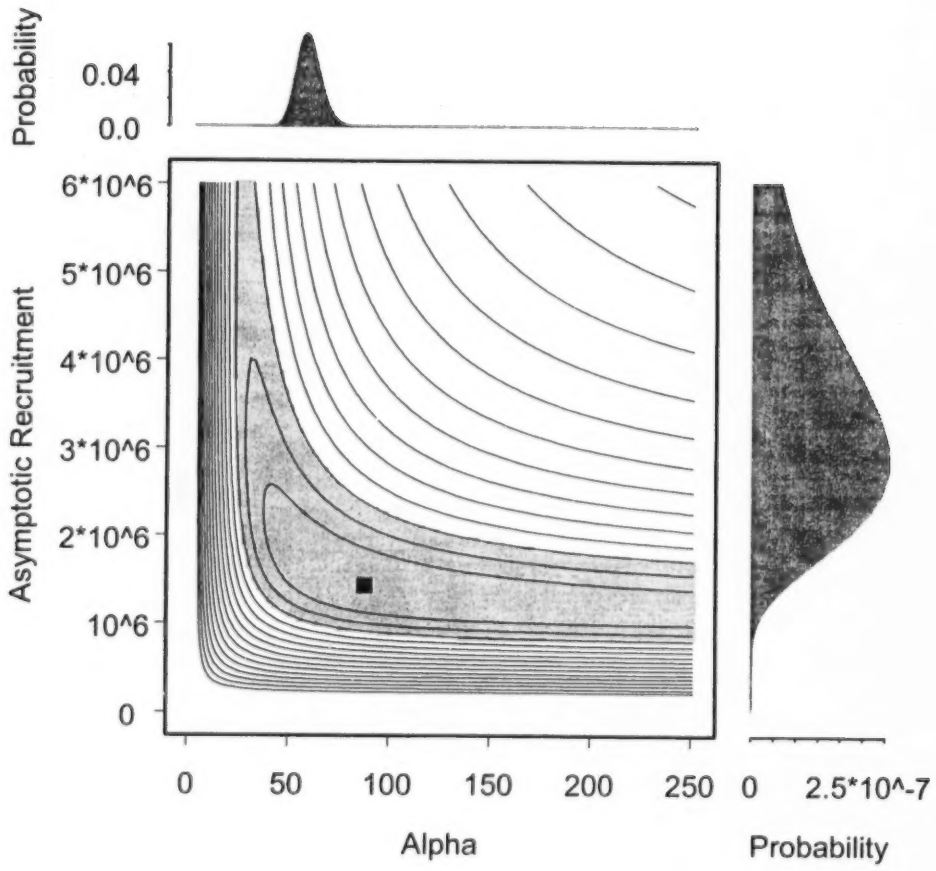

Figure 16. A comparison of the log-likelihood surface for alpha and the asymptotic recruitment level for the Gaspereau River alewife population (lower left panel) and the mixed effects model random effects distributions for alpha (top panel) and the asymptotic recruitment level (right panel). The black square shows the point where the log-likelihood is maximized.

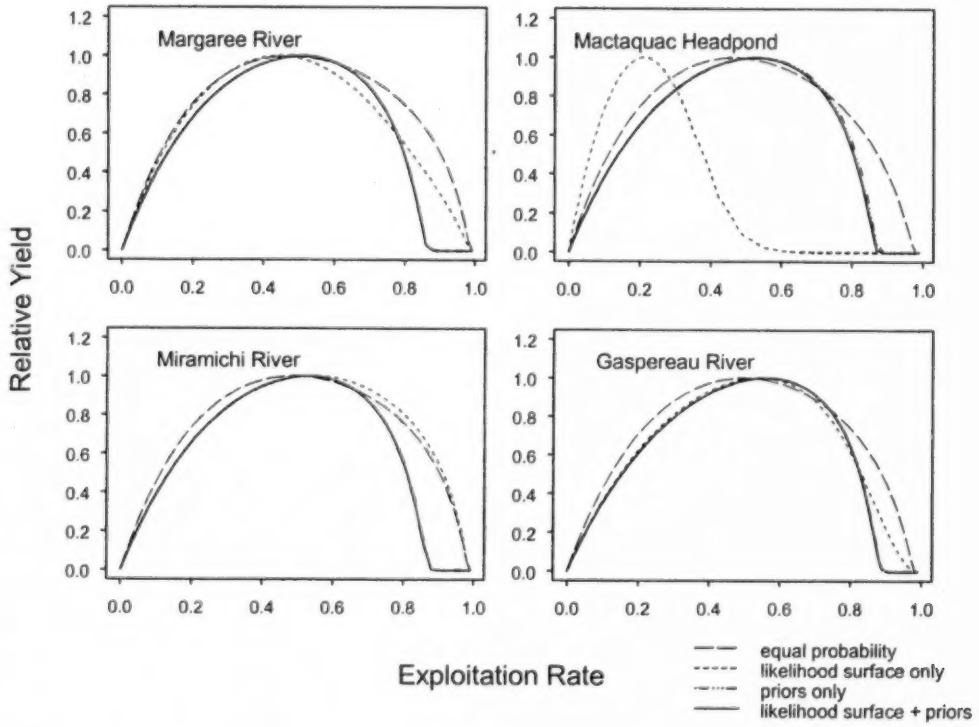

Figure 17. The relationship between exploitation rate (u) and the expected yield obtained by integrating across the probability surface for alpha (α) and the asymptotic recruitment level (R_0) for each level of u, for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations. The probability surface was calculated using four methods: assuming each point in the probability space is equally likely, using the joint likelihood surface for α and R_0, using only the prior distributions for α and R_0 obtained from the mixed effects model, and using the joint posterior distribution. Yields are reported relative to the maximum yield obtained using each method.

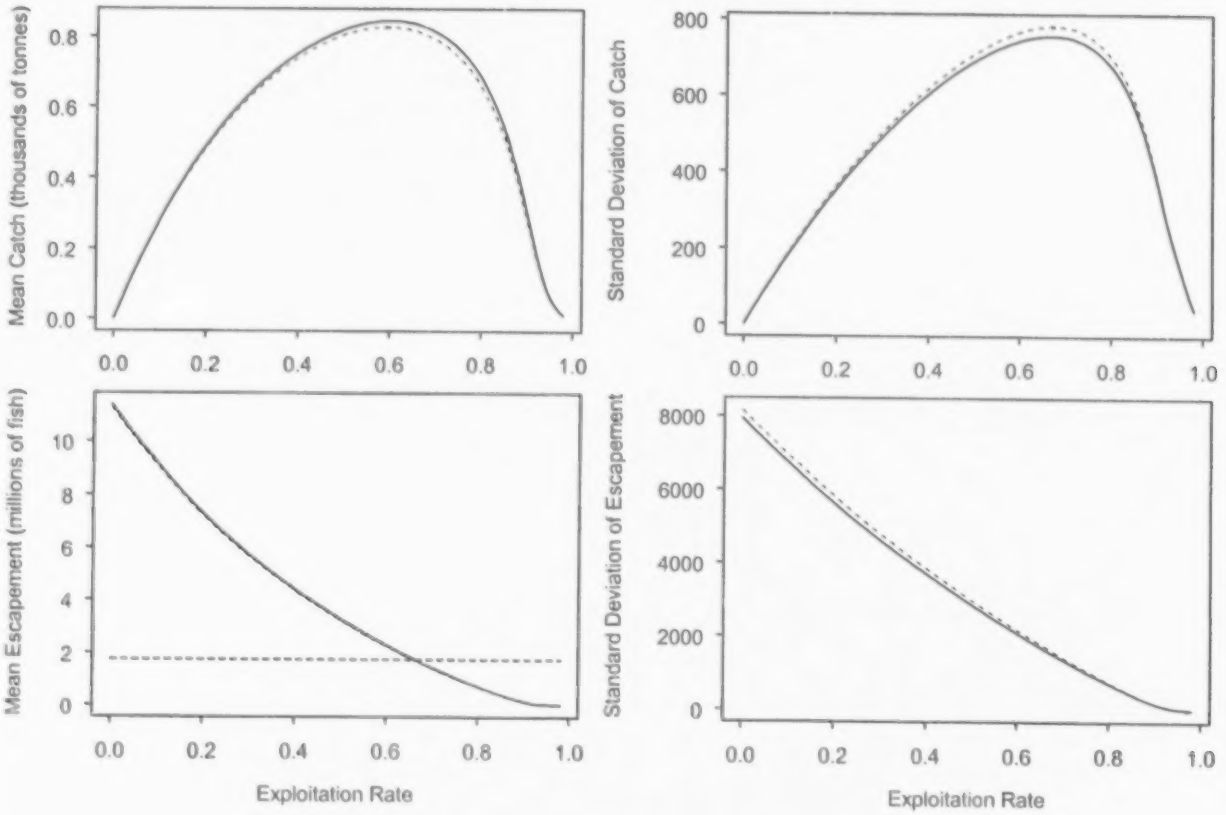

Figure 18. Comparison of simulation results for the Margaree River using constant (solid lines) and variable (dashed lines) maturity schedules. The lines give the means of the summary statistics (mean and standard deviation) for the catch and spawning escapement for a 50 year time period. The means are calculated from 100 simulations at each exploitation rate (0.0 to 0.99 with an increment of 0.01). The horizontal dashed line in the lower, left plot is the spawning escapement that gives maximum sustainable yield.

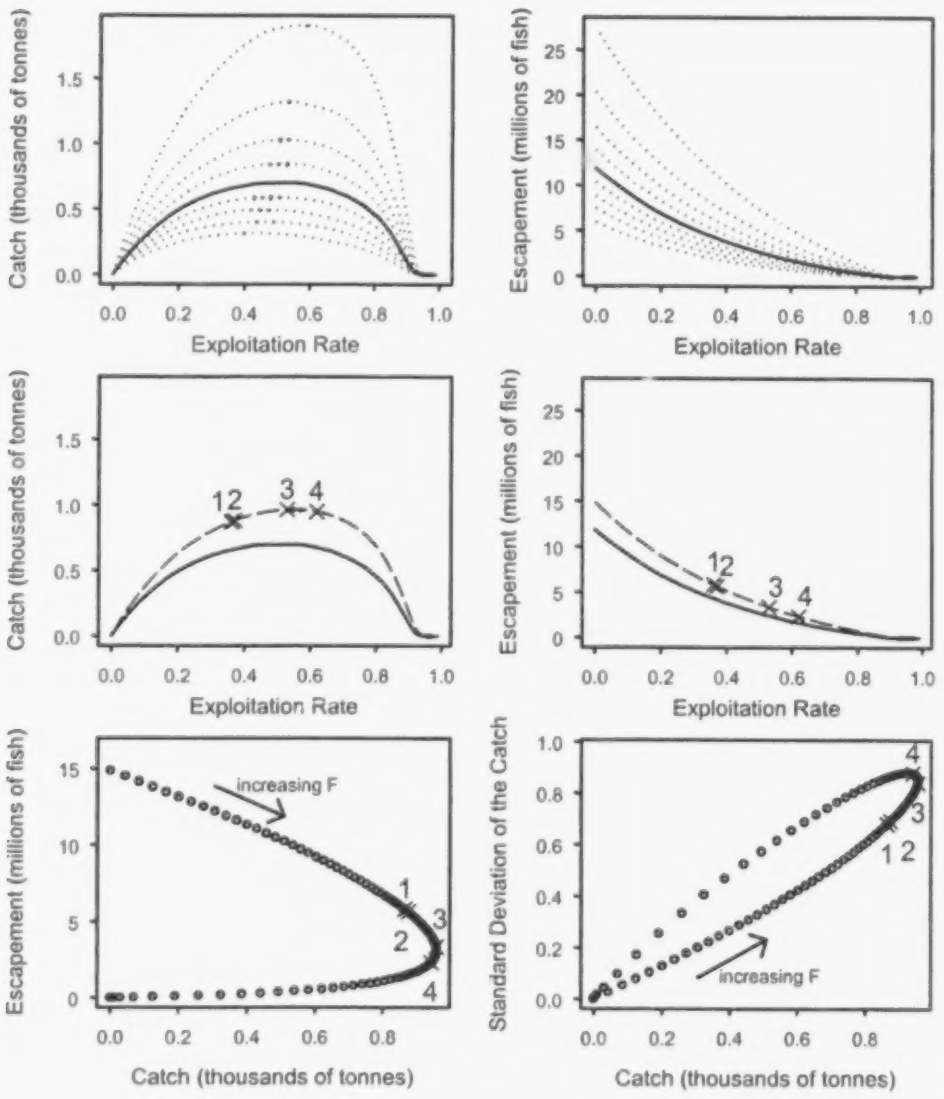

Figure 19. A summary of the simulation results for the Margaree River alewife population. Each plot summarizes 100 population projections (50 year duration) at each exploitation rate,*u*, (0.0 to 0.99 with an increment of 0.01). The solid line in the upper two plots are the median catch and spawning escapements as a function of *u*. The dashed lines are the 10th to 90th percentiles (bottom to top lines) of the catch and spawning escapements. The middle two plots show the median (solid lines) mean (dashed lines) catch and spawning escapement as a function of *u*. The points are the exploitation rates corresponding to 1: $F_{90\%max.med}$, 2: $F_{35\%}$, 3: $F_{max.E(C)}$, and F_{msy}. The bottom left plot shows the relationship between spawning escapement and catch. Each point represents the mean of 100 simulations at each exploitation rate (the uppermost point is $u = 0.00$, and *u* increases by 0.01 to a maximum of 0.99 in the lower left corner). The lower right plot shows the relationship between the standard deviation of the catch and the catch for each *u*.

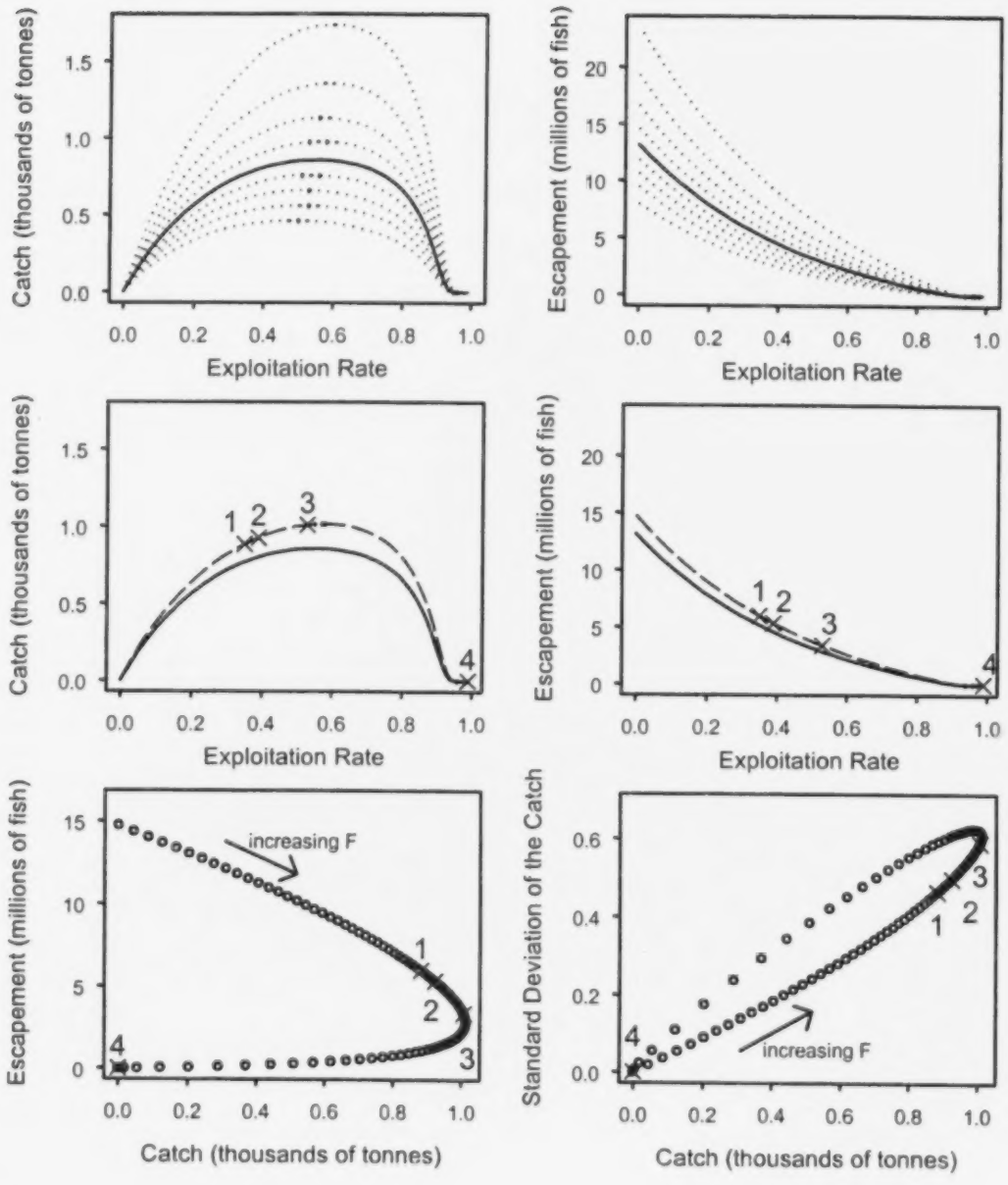

Figure 20. A summary of the simulation results for the Miramichi River alewife population. Line and point symbolism are explained in the caption for Figure 19.

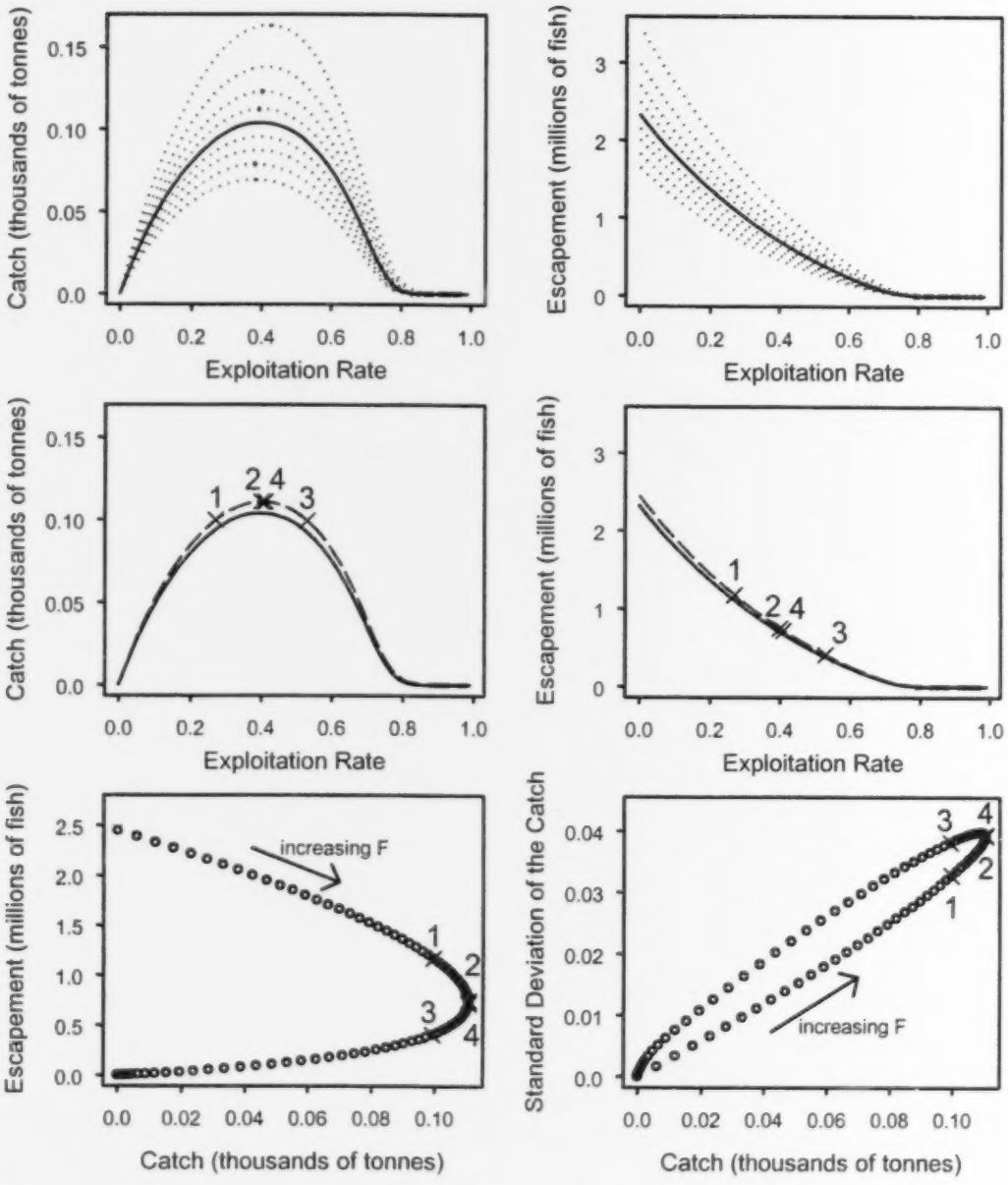

Figure 21. A summary of the simulation results for the Mactaquac Headpond alewife population. Line and point symbolism are explained in the caption for Figure 19.

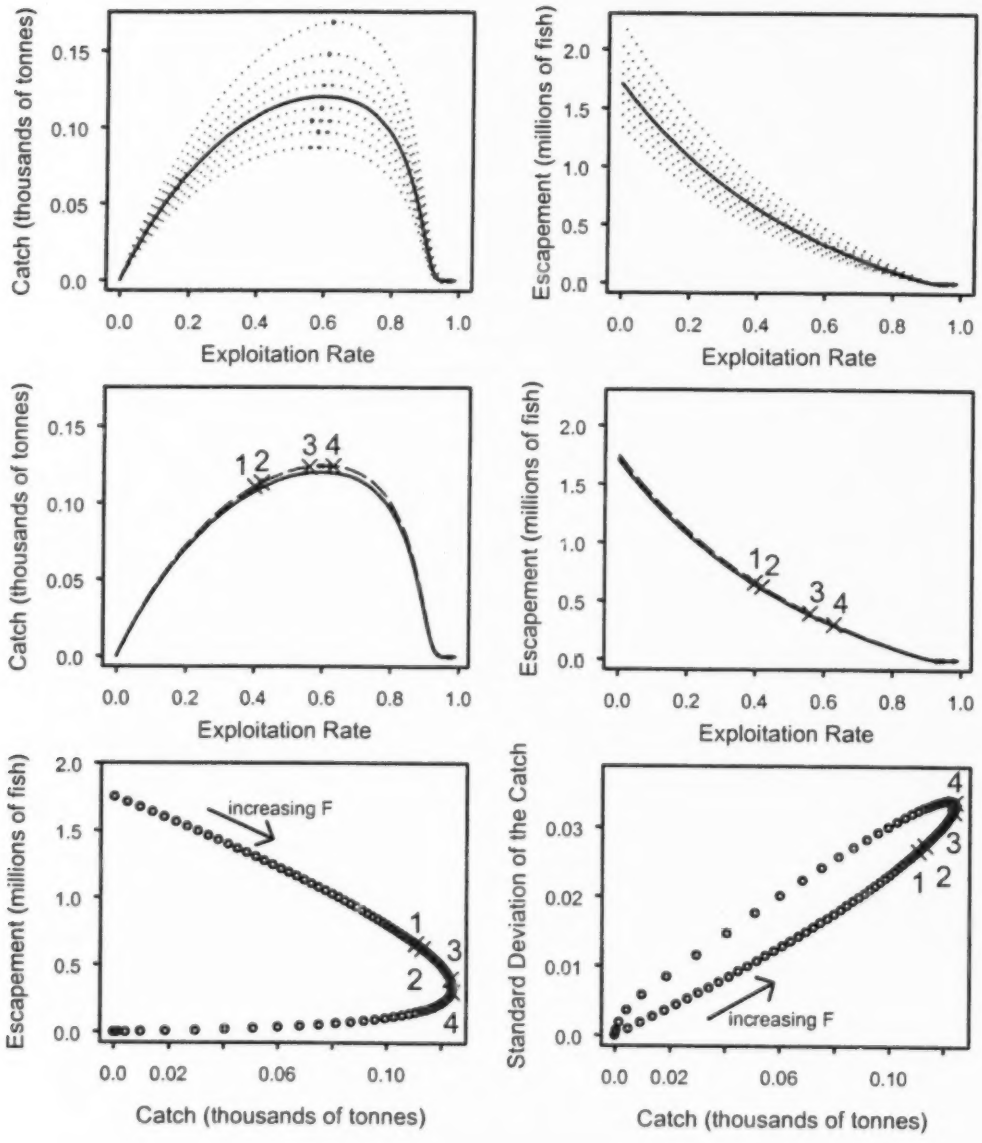

Figure 22. A summary of the simulation results for the Gaspereau River alewife population. Line and point symbolism are explained in the caption for Figure 19.